

**IMPACTS OF SEDIMENTATION ON THE
STRUCTURE AND FUNCTIONING OF
AGRICULTURAL STREAM COMMUNITIES**

A thesis submitted in partial fulfilment of the requirements for the

Degree

of Doctor of Philosophy in Ecology

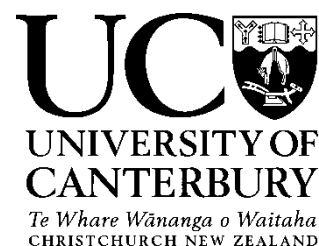
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by Francis J. Burdon

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A handwritten signature in black ink, appearing to read 'Jon S. Harding'.

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THESIS ABSTRACT

The excessive deposition of fine inorganic sediment (<2 mm) is a major pathway by which agricultural land uses exert pressure on stream ecosystems. However, less well understood are the underlying mechanisms driving threshold biotic responses and the ecological consequences of community changes to sedimentation. Reviewing the literature, I found that sedimentation can affect algal and detrital pathways, and invertebrate community composition may show abrupt shifts with increased sediment. Moreover, functional changes to communities potentially leads to simpler food webs, with altered interactions and decreased ecosystem function. After identifying these knowledge gaps, I conducted survey and experimental research using agricultural streams on the Canterbury Plains of New Zealand's South Island. Results from my survey of 30 streams along a sedimentation gradient showed that pollution-sensitive invertebrates (% EPT; Ephemeroptera, Plecoptera, Trichoptera) demonstrated threshold responses to sediment that varied with spatial scale, and change-point analysis indicated marked declines beyond 20% fine sediment covering streambed reaches. Structural equation modeling indicated that decreased habitat availability was a key mechanism contributing to these changes. To better understand the functional consequences of altered community structure, I investigated food webs in 12 streams along the gradient. The results showed a compression of community trophic niche space, suggesting that in particular, primary consumers became trophically more equivalent. The simplification of stream food webs with increasing sediment appeared to be the result of functional changes to invertebrate communities, with fewer specialised consumers, and shifts in the availability of basal resources. Using field and laboratory experiments investigating litter breakdown and invertebrate feeding, I found that the net consequence of functionally less diverse stream communities with increased sediment was impaired ecosystem function, demonstrated by

a reduction in litter breakdown rates. The reduction of detrital resource availability through burial by sediment in laboratory mesocosm experiments strongly influenced detrital consumption rates, thus leading to reduced growth and survival of detritivorous caddisflies. The survey and experimental results support my postulate that sediment deposition causes environmental stress by degrading benthic habitat and making associated food resources (e.g., periphyton and leaves) less available. Overall, my results have provided new insights into sediment impacts on stream communities and have furthered our understanding of how these changes affect the structure and functioning of stream ecosystems.

PREFACE

This thesis addresses the potential influences of stream sedimentation at multiple levels of biological organisation (e.g., communities, food webs, and ecosystems). I postulated that sediment deposition alters ecosystem structure, makes habitat and associated food resources less available through burial, and increases substrate instability, thus contributing to greater environmental stress and concomitant changes at the community level (e.g., stream macroinvertebrate communities). These structural changes were expected to also influence higher levels of biological organisation incorporating food webs and ecosystem processes, leading to altered stream functioning. Chapters 1-4 have been written as stand-alone journal manuscripts, meaning there is some repetition of concepts and cited literature. However, to enable the reader to easily navigate between sections, I have provided short preambles at the beginning of each data chapter to help highlight the flow of ideas. Moreover, the manuscript form of this research requires a significant amount of material to be relegated to the appendices for each chapter.

In the Chapter 1 literature review, I emphasise the need to understand responses to sedimentation at multiple levels of biological organisation. Underpinning this approach, I have considered three fundamental questions: (1) Does sedimentation influence structural changes in stream communities?, (2) Do changes to communities affect food-web properties?, and as a consequence, (3) Does ecosystem function change? These questions in turn help to structure the following three data chapters of my thesis. In many instances, the paucity of studies specifically focusing on sediment effects at higher levels of biological organisation (e.g., food webs) has required inference to be drawn from theory in the literature review (Chapter 1). Thus, in Chapter 1, I have synthesised the available peer-reviewed literature with current theory. Moreover, by identifying apparent gaps in our knowledge, I have then followed up in later chapters with my own observational and experimental PhD

research. In particular, the potential for non-linear (e.g., threshold) responses to sediment deposition by stream invertebrate communities are reviewed, with known values from previous studies reported. These threshold responses can reflect a change in community structure from an assemblage dominated by mayflies and caddisflies to one characterized by worms, snails, and micro-crustaceans (Waters 1995). Better describing threshold responses and understanding the potential underlying mechanisms influencing these non-linear changes in community structure directly links the review to the next chapter. Chapter 1 has been submitted for publication as a co-authored paper with my main supervisor and I have received referees comments.

Chapter 2 focuses on the question: Are there structural changes to stream communities in response to sedimentation? Although the answer to the question would seem axiomatic, it is fundamental to establish the potential influences of sedimentation on community structure (Jones et al. 2012). This is particularly important for my study, given the agricultural context and the potential for multiple stressors affecting streams communities (Townsend et al. 2008). Moreover, this study seeks to elucidate threshold responses by invertebrate communities to deposited sediment, and to better understand the underlying mechanisms. To test this I surveyed 30 streams on the Canterbury Plains along gradients of deposited sediment and dissolved nutrients (e.g., nitrate). This chapter has been submitted as a co-authored paper with both my supervisors and is “*in press*” in Ecological Applications (Burdon et al. *in press*).

Chapter 3 considers the question: Do changes to communities affect food-web properties? Although previous studies have considered the effects of sediment on community structure and function, this has often been done using invertebrate or fish data alone. Few studies have attempted to characterize entire food webs and their response to sedimentation (Jones et al. 2012), let alone synthesizing previous knowledge with ecological theory to make

predictions about sediment impacts. This study links in with many of the predictions discussed in the review chapter, and focuses on three key predictions: sedimentation affects (1) food-chain length (i.e., vertical structure), (2) effective resource breadth (i.e., horizontal structure), and consequently, (3) community trophic niches in stream ecosystems. To evaluate these predicted effects, I surveyed stream food webs along a sedimentation gradient in a subset of 12 sites from the study in Chapter 2, using stable isotopes of carbon and nitrogen. To better understand the underlying mechanisms potentially influencing my main results, I also collected and analysed complementary community and ecosystem data. This included invertebrate functional-feeding groups, and basal resource quality and availability. I have written this chapter as the primary author, but it has not been submitted to a journal.

Chapter 4 links to previous chapters by considering the question: Does ecosystem function change in response to sedimentation? One of the challenges ecologists face is linking the effects of biodiversity to ecosystem function (Cardinale et al. 2012). Using food webs as a systems approach representing patterns of biodiversity and energy flow helps to link factors affecting communities to those controlling ecosystem processes (Thompson et al. 2012). However, there are limits to what this approach can tell us, and in Chapter 3 it is not clear whether sedimentation weakens consumption of coarse detrital material. Moreover, despite the ubiquity of sediment impacts in streams affected by human land uses and the importance of the detrital pathway to stream ecosystems, sediment influences on litter decomposition remain poorly understood, and the results that have been reported in the literature are often equivocal (Niyogi et al. 2003). Thus, using detrital processing as a model ecosystem function, I consider the potential influences of sediment at the ecosystem scale. To test this, I performed litter breakdown assays in nine streams along a sediment gradient using three difference leaf-pack treatments (exposed, protected, and buried). To further investigate mechanisms contributing to these results, I also conducted laboratory mesocosm experiments

testing the effects of sedimentation on consumer-resource interactions using leaf litter and detritivorous caddisflies. I have written this chapter as the primary author, but it has not been submitted to a journal.

The final chapter (5) summarizes the previous four chapters and adds further discussion where appropriate, whilst providing some directions for future research. This chapter also highlights some potential management implications of sedimentation in streams.

LITERATURE CITED

- Burdon, F. J., A. R. McIntosh, and J. S. Harding. *in press*. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. *Ecological Applications* doi:10.1890/12-1190.1.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59-67.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055-1071.
- Niyogi, D. K., K. S. Simon, and C. R. Townsend. 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology* 48:1698-1708.
- Thompson, R., U. Brose, J. Dunne, R. Hall, S. Hladyz, R. Kitching, N. Martinez, H. Rantala, T. Romanuk, and D. Stouffer. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution* 27:689-697.

Townsend, C. R., S. S. Uhlmann, and C. D. Matthaei. 2008. Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology* 45:1810-1819.

Waters, T. F. 1995. Sediment in streams. sources, biological effects, and control. American Fisheries Society, Bethesda, Maryland, USA.

CHAPTER 1

SEDIMENTATION AND STREAM ECOSYSTEMS: A REVIEW OF IMPACTS ON COMMUNITY STRUCTURE AND FUNCTIONING



A stream with intermediate sedimentation located near Rangiora, Canterbury Plains.

Abstract. Inorganic fine sediment pollution is a widespread and pervasive problem globally, and is a major pathway whereby agriculture exerts pressure on aquatic ecosystems. Sediment occurs naturally in streams but becomes an ecosystem stressor when inputs exceed ‘assimilative capacity’. Sedimentation can alter ecosystem structure by degrading habitat, potentially leading to reduced substrate stability and heterogeneity, and these changes may cause direct and indirect effects across multiple trophic levels in stream food webs. At the basal level, sediment can decrease algal production and reduce autotrophic biomass, leading to the dominance of heterotrophy. Detrital pathways can be affected by reduced microbial activity and resource availability via burial by sediment. The direct effects of physical stress, coupled with the more indirect effects of reduced food and habitat may alter growth, recruitment, emigration, and mortality rates of consumers. Numerous studies have shown that benthic invertebrate communities change in response to sedimentation, and shifts in community composition can be abrupt, with mean values of reported threshold values ranging from 10–20% deposited sediment. Reduced species populations can influence the next trophic level via diminished transfers of energy, and these effects may propagate across stream boundaries affecting riparian predators and reciprocal linkages of prey. Although food-web properties such as food-chain length may be a poor indicator of change, functional-feeding groups that integrate different energetic pathways can be disproportionately affected by sediment, leading to simpler food webs and decreased ecosystem function. Recognising how sediment affects lotic communities across multiple levels of biological organisation, along with robustly quantifying thresholds of harm, is critical in a changing world if we are to preserve biodiversity and ecosystem function.

Keywords: agriculture; ecosystem function; fine inorganic sediment; global change; resource subsidies; sediment thresholds; stream communities; stream food webs

INTRODUCTION

Streams and rivers are open ecosystems that are characterised by the dynamic flux of energy, matter, and organisms between land and water (Ward 1989). In particular, as water works its way downstream, it imparts some of its energy on the transport and rearrangement of materials along the stream's boundaries (Gordon et al. 2004). The presence of suspended and moving sediment is predominantly transient, as it enters and leaves the fluvial channel only to be again eroded away and transported further downstream. Most natural sediment inputs can be accommodated by stream processes, but excessive anthropogenic inputs often exceeds the 'assimilative capacity' of streams (Cairns 1977, Waters 1995). This can harm stream biota, thus leading to anthropogenic fine inorganic sediment (sediment hereafter; particles <2 mm) being characterised as a stressor of lotic ecosystems (Waters 1995, Matthaei et al. 2006). However, despite the widespread prevalence of sediment pollution (Wood and Armitage 1997), there are still gaps in our knowledge of its effects at multiple levels of biological organisation (e.g., communities, food webs, and ecosystems).

Sedimentation in streams has been attributed to various human activities, including mining (Davies-Colley et al. 1992), production forestry (Death et al. 2003), road construction (Cline et al. 1982), and urbanisation (Waters 1982). However, the most widespread impacts are associated with non-point source pollution arising from agriculture (Pimentel et al. 1987, Walling 1990). Agriculture is the dominant human land use, occupying the largest proportion of area in many catchments (Allan 2004), and numerous studies have associated declines in water and habitat quality with detrimental changes to biotic communities (Quinn and Hickey 1990, Allan et al. 1997, Sponseller et al. 2001). Moreover, agriculture must intensify to support population growth, meaning excessive demands on finite resources (e.g., water availability) may

contribute to habitat simplification, loss of ecosystem services, and species extinctions (Vitousek et al. 1997, Tilman et al. 2001, Pimentel et al. 2004).

Agriculture land uses degrade streams by changing habitat, decreasing bank stability, altering flows, and by increasing diffuse inputs of pollutants such as sediment (Allan 2004). This can be a consequence of cropping (Zimmerman et al. 2003), overgrazing (Armour et al. 1991), stock intrusion (Herbst et al. 2012), and riparian disturbance (Jones et al. 1999). Agricultural streams are often heavily modified, and channel straightening can lead to more uniform and diffuse deposition of sediment (Harrison et al. 2004). Low flows resulting from drought and water abstraction for irrigation can lead to increased sediment deposition through reduced water velocities (Wood and Armitage 1999). Across the United States, risk of stream biological impairment doubled with increasingly diminished flows (Carlisle et al. 2010), which can reduce the flux of deposited sediment causing greater ecological harm through increased deposition (Matthaei et al. 2010). Cumulatively, these changes may have long-lasting legacy effects on aquatic biodiversity (Harding et al. 1998), and may negatively impact receiving environments such as lakes (Donohue and Molinos 2009).

Major reviews assessing drivers of global change in freshwater ecosystems have focused on the effects of biodiversity loss (Dudgeon et al. 2006), eutrophication (Smith et al. 1999), and warming (Woodward et al. 2010), whereas recent reviews of sediment influences on lotic habitats have focused on specific communities such as fish and macroinvertebrates because of the paucity of studies assessing food web and whole ecosystem effects (Kemp et al. 2011, Jones et al. 2012). Food webs are a robust systems approach representing patterns of biodiversity and energy flow in a quantifiable framework amenable to comparative analyses (Thompson et al. 2012). Because food webs reflect multiple levels of biological organisation, (individuals,

communities, and ecosystems), they can better predict ecosystem responses because of the potential for emergent properties to be manifested in these more complex systems (Woodward et al. 2010). Perturbations can have both direct and indirect impacts on biological systems, and impacts at lower levels of organisation (e.g., populations) may permeate throughout the food web, thus affecting ecosystem functioning (Woodward 2009). In this paper, we aim to review responses to sedimentation at multiple levels of biological organisation. Underpinning this approach, we have considered three fundamental questions: (1) Does excessive sediment deposition influence structural changes in stream communities? (2) Do changes to communities affect food-web properties? and (3) Does ecosystem function change?

PHYSICAL DISTURBANCE: SEDIMENT

Effects of disturbance strongly shape lotic communities, and are generally classified as either ‘pulse’ or ‘press’ events that can be natural or anthropogenic (Resh et al. 1988, Lake 2000). Pulse disturbances have transient effects because of relatively discrete impacts (Fig. 1a). Hydrological disturbance, characterised by floods and extensive bed movement, epitomise pulse disturbance, although the resilience of stream biota means that effects are often short-lived (Scrimgeour et al. 1988). In contrast, press disturbances are long-term, with sustained impacts on streams (Fig. 1b), often resulting from changes to the physical structure of the ecosystem. Lenat et al. (1979) described the situation where sedimentation exceeded the ‘assimilative capacity’ of a stream as the difference between ‘habitat reduction’ and ‘habitat change’. We consider deposited sediment that exceeds the ‘assimilative capacity’ of streams to be a press disturbance; referred to hereafter as ‘sedimentation’.

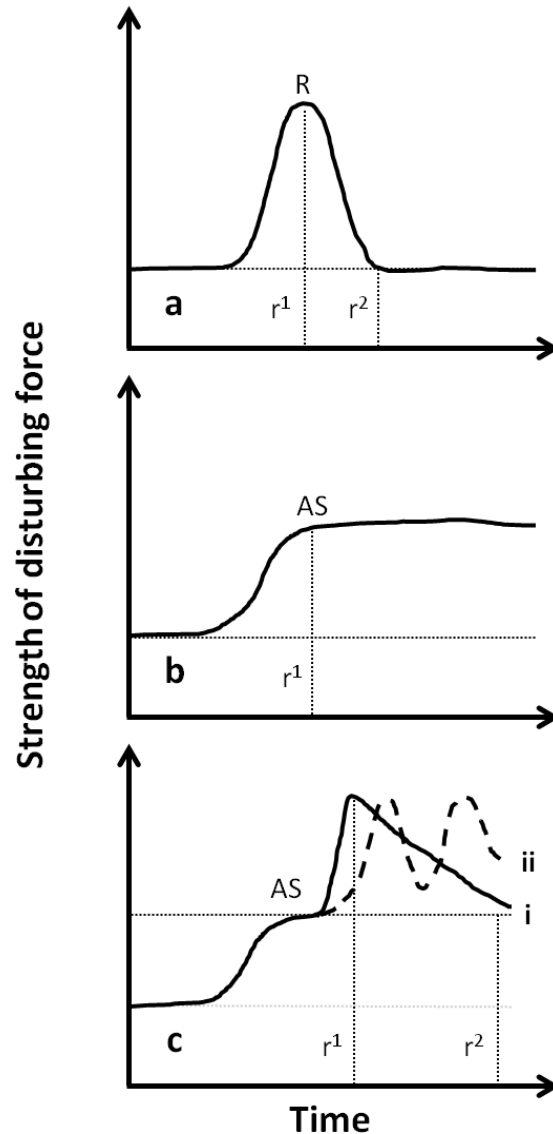


FIG. 1. Three types of stream disturbance: (a) pulse, (b) press, and (c) press-pulse; adapted from Lake (2000). These demonstrate the differences in temporal trends and the magnitude of the disturbing force (i.e., inputs of sediment). (a) An archetypal pulse disturbance shows the difference between the resistance (R) and the resilience ($r = r^2 - r^1$) of the system. (b) A press disturbance may force the system into an alternate state (AS). (c) Perturbations that combines elements of press and pulse disturbance. The effects of press disturbance may lead to lower resilience to pulse disturbances (i), or a decrease in the stability of the system (ii). These may be generated by deviations from normal conditions as mediated by hydrological disturbance (floods, droughts, flow regulation) and land-use change (forest to agriculture).

The recovery of a stream from press disturbances such as sedimentation can take many years and may require human intervention to restore the system to a natural state (Wood & Armitage 1997). These two types of disturbance ('pulse' and 'press') can interact synergistically, and may lead to less resilient and stable ecosystems (Fig. 1c), thus affecting community and food-web dynamics. The effects are similar to a "ramp" disturbance (Lake 2000), and at the patch and reach scale may result from saltation (sliding and bouncing) of sediment particles (Culp et al. 1986) and persistent sediment bed-loads (Molinos and Donohue 2011); at larger spatial scales these synergies may also reflect changes in land use that increase catchment sediment inputs and alter hydrology (Collier and Quinn 2003).

As a caveat, theory on multiple stressors suggests that adsorbed nutrients and toxic compounds on inorganic particles may also produce complex outcomes (Folt et al. 1999), but are mainly outside the scope of this review; also see Wood and Armitage (1997) for a more extensive discussion of sediment quality. In the following section, the key sediment pathways that affect different groups of stream organisms (periphyton, bacteria/fungi, invertebrates, and fish) are reviewed; these effects are summarised in Fig. 2.

SEDIMENT EFFECTS ON STREAM COMMUNITIES

Periphyton

Periphyton is highly sensitive to increased turbidity, scouring bed-loads, and deposited sediment (Cline et al. 1982, Davies-Colley et al. 1992, Yamada and Nakamura 2002). The turbidity of water increases with suspended sediment concentrations, thus impairing light penetration and reducing algal growth (Davies-Colley et al. 1992). Sediment can be incorporated into periphyton and decrease chlorophyll-*a* concentrations, thus leading to a reduction in the

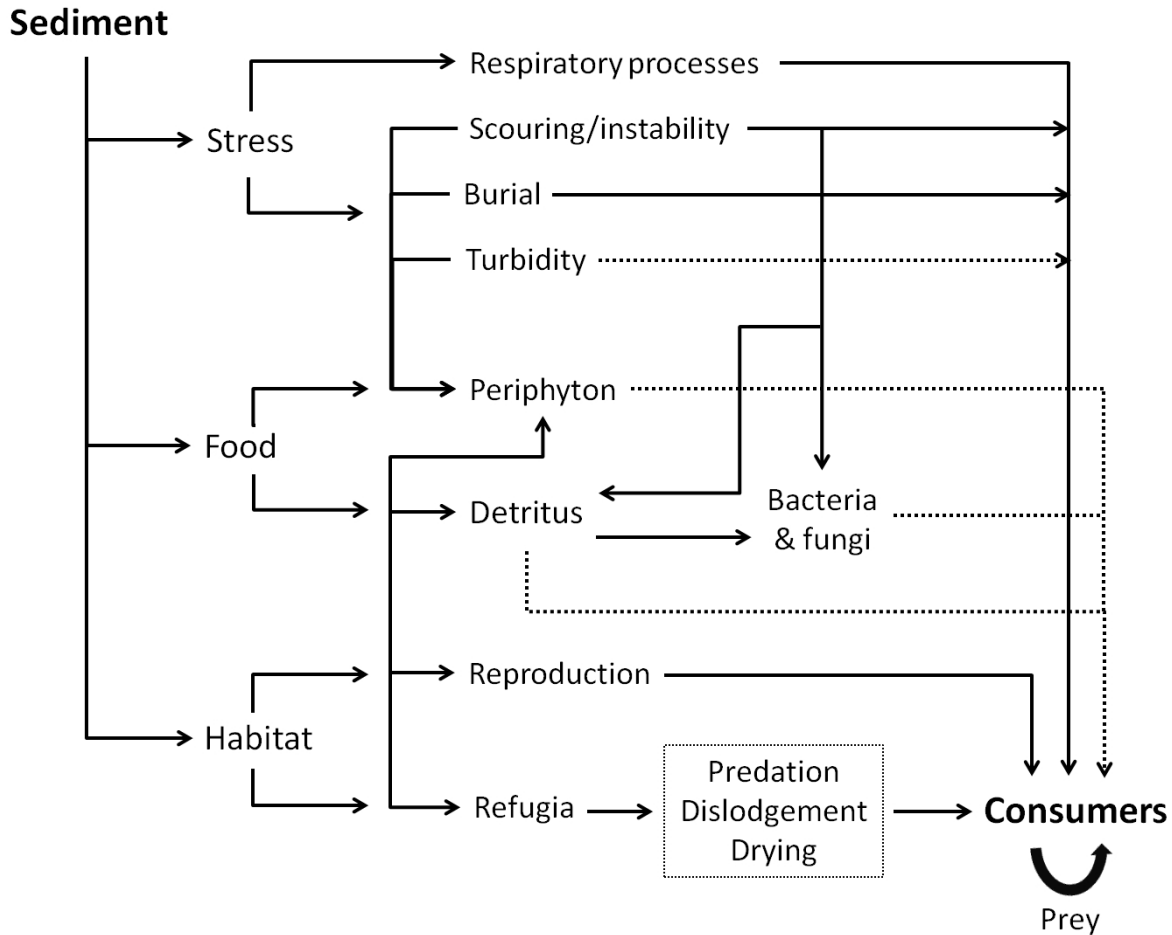


FIG. 2. Major pathways of sediment disturbance affecting stream communities. Prey reduction as a consequence of sediment disturbance can additionally affect consumers. Dotted lines are used to help distinguish pathways. For further explanations see text.

autotrophic content (Graham 1990, Yamada and Nakamura 2002). Kent and Stelzer (2008) suggested that sediment affected periphyton stoichiometry by increasing the proportion of carbon to nitrogen and phosphorous, thereby reducing nutritional quality (*cf.* Molinos and Donohue 2009). Sediment may alter algal community composition and lead to reduced diversity (Cline et al. 1982). One mechanism driving changes to algal community composition is by sediment deposition, which can favour motile unicellular diatoms and filamentous cyanobacteria that use their mobility to maintain a favourable position in unstable sandy substrates (Biggs 2000,

Dickman et al. 2005). In contrast, periphyton communities with a tightly adherent and cohesive mat physiognomy may be more resistant to the scouring effect of suspended sediment, although abrasion by suspended particles or bed load generally reduces periphyton biomass and changes community composition (Francoeur and Biggs 2006).

Bacteria and fungi

Fine sediment substrate can be important zones of organic matter processing by bacteria (Rier and King 1996, Romani and Sabater 2001), but there is evidence that physical disturbance through substrate instability and burial can negatively affect microbial communities (Atkinson et al. 2008, McTammany et al. 2008, Gücker et al. 2009). Shifts to heterotrophy with fine sediment have been shown in studies of stream ecosystem metabolism (Rier and King 1996, Atkinson et al. 2008). However, physical disturbance associated with bed movement in silted agricultural streams may reduce benthic microbial biomass, and lead to reduced ecosystem respiration (Atkinson et al. 2008, Gücker et al. 2009). Furthermore, sediment can create hypoxic conditions and reduce the surface area of organic matter for microbial colonization (Pascoal et al. 2005), and the respiration of microbes on wood has been negatively correlated with deposited sediment (McTammany et al. 2008). Bacterial community composition on leaves has been shown to be affected by sedimentation, with greater proportions of anaerobic taxa at sediment-impacted sites (Newman 2011). Similarly, additions of very fine sediment slightly reduced fungal assemblage richness and the sporulation rate of three fungal species in a laboratory study (Sanpera-Calbet et al. 2012).

Invertebrates

The sedimentation-induced changes to stream invertebrate communities have often been characterized as a shift from assemblages of mayflies, stoneflies, and caddisflies (EPT) to an

alternative state dominated by snails, chironomids, and oligochaetes (Waters 1995). Sediment can reduce invertebrate densities and diversity (Angradi 1999, Matthaei et al. 2006), although rarefaction procedures have shown that the latter can be due to reduced abundances (Vasconcelos and Melo 2008). Sediment affects stream invertebrates through multiple pathways (Fig. 2); for a more extensive review see Jones et al. (2012). In summary, these include direct effects on respiratory processes (Lemly 1982) and filter-feeding (Aldridge et al. 1987), burial by sediment (Wood et al. 2005), and increasing drift due to sediment deposition or substrate instability (Culp et al. 1986, Larsen and Ormerod 2009). Sediment deposition may disproportionately affect hyporheic communities through infilling of interstitial habitat and decreased oxygen flow (Richards and Bacon 1994). More indirect effects can be induced by the reduction of food resources quality and quantity such as periphyton (Suren 2005). Grazing insects preferentially consume uncontaminated periphyton, and growth rates can be impaired when fed periphyton with a high inorganic proportion (Ryder 1989, Peeters et al. 2006).

However, the most pervasive effect of sediment comes through deposition which can alter the physical structure of the streambed through the removal of habitat, potentially reducing substrate heterogeneity and refugia from hydrological disturbance and predation (Wood and Armitage 1997, Jones et al. 2012). Numerous studies have identified deposited sediment thresholds, but these have often been measured at different scales using various invertebrate responses and analytical methods, which likely influence the results and reduce their general applicability (Table 1). The exact proportion of habitat thresholds can be influenced by the spatial 'grain' size of sampling, thus suggesting scale should be considered when elucidating these values (Wiens 1989, Homan et al. 2004). This is important because studies have shown regime shifts in response to habitat loss (Pardini et al. 2010), and crossing abrupt transitions may

lead to alternative states such as different community assemblages (Scheffer et al. 1993, 2001). Identifying realistic deposited sediment thresholds is important, given most current management guidelines are based on suspended sediment targets, and thus are unlikely to be appropriate for invertebrate communities (Jones et al. 2012).

TABLE 1. Published deposited sediment thresholds for benthic invertebrate communities in streams and rivers at two different spatial scales, reach and patch. % Sed., the relative proportion of deposited fine inorganic sediment (< 2 mm grain size); SS, sediment-sensitive taxa; EPT, pollution-sensitive stream-insect orders (Ephemeroptera, Plecoptera, Trichoptera); interstitial sediment, sediment as a proportion of total substrate mass (in contrast to % cover stated in other examples).

Scale	% Sed.	Country	Region	Reference	Comments
Reach	9.7	USA	Western States	(Bryce et al. 2010)	Survey, 8 SS taxa
	14.8	Canada	New Brunswick	(Benoy et al. 2012)	Survey, %EPT
	19.6	USA	Southwestern States	(Jessup et al. 2010)	Survey, 'Mountain' streams, SS 'clinger' taxa
	30	USA	Pacific Northwest and Idaho	(Relyea et al. 2000)	Survey, absolute limits, 7 SS taxa
<i>Mean</i>	18.5				
Patch	5	NZ	Otago	(Wagenhoff et al. 2012)	Experiment, EPT densities
	7.1	UK	Wales	(Larsen et al. 2009)	Survey, median EPT taxa, 50% abundance,
	13.3	Canada	New Brunswick	(Benoy et al. 2012)	Survey, %EPT, interstitial sediment
	14.5	NZ	Otago	(Ryder 1989)	Experiment, 1 SS taxon, interstitial sediment
<i>Mean</i>	10.0				

Fish

The impacts of sediment on fish have long been recognised by fisheries biologists (Cordone and Kelly 1961). The direct effects of increased suspended sediment on fish include the clogging of gills (Herbert and Merckens 1961); and a reduction in water clarity due to increased turbidity can affect feeding and migratory behaviour (Boubee et al. 1997, Rowe and Dean 1998, Shaw and Richardson 2001). Changes in fish community composition may reflect feeding mode and reproductive biology (Berkman and Rabeni 1987, Sutherland et al. 2002). Sedimentation directly affects fish that rely on benthic substrate to spawn, with negative impacts of deposition on the development of eggs and the successful recruitment of fry (Wood and Armitage 1997). Sediment deposition can result in reduced hydraulic exchange, leading to lower levels of dissolved oxygen and impaired exfiltration of metabolic wastes in the streambed (Brunke and Gonser 1997). Meta-analysis indicates that when the percentage of intra-gravel sediment exceeds 10%, salmonid egg survival can rapidly decrease (Jensen et al. 2009). Reduction of prey through sedimentation can affect growth rates, survival, and distributions of stream fishes (Osmundson et al. 2002, Suttle et al. 2004).

SYNTHESIS USING A FOOD-WEB PERSPECTIVE

Food-chain length

The paucity of studies specifically addressing sediment impacts on stream food webs necessitates inference to be drawn from ecological theory. A fundamental structural feature of any food web is food-chain length (FCL), and is commonly defined as the number of transfers of energy or nutrients from the base to the top of a food web (Post 2002). Sedimentation may shorten FCL through reduced algal production (Yamada and Nakamura 2002), decreased invertebrate biomass (Angradi 1999), and reduced abundances of preferred prey (Osmundson et

al. 2002, Suttle et al. 2004). Perturbations that act at the base of the food web can affect consumers in higher trophic levels (Petchey et al. 2004), and the productivity hypothesis states that FCL should increase with greater basal production (Pimm 1982). This is related to the trophic-dynamic concept which describes energy transfer inefficiencies across trophic levels (Lindeman 1942). Townsend et al. (1998) found that algal productivity was strongly correlated with FCL, and the removal of basal resources in a detrital-based stream system resulted in the loss of top predators (Wallace et al. 1997). An example from the sediment literature showed that the abundance of the endangered Colorado pike-minnow (*Ptychocheilus lucius*) was related to the availability of suitable prey fish, which may be limited by standing crops of periphyton and macroinvertebrates reduced by sediment (Osmundson et al. 2002). This suggests that sedimentation may result in a 'bottom-up' trophic cascade affecting FCL.

In contrast, the dynamic constraints hypothesis posits that disturbance disproportionately affects higher trophic levels, thus reducing FCL. Because species higher in the food chain are rarer, they are more likely to be lost from the system during a disturbance event (Thompson and Townsend 2005). Theoretical models of simple food chains have shown that longer chains are less resilient, thus more unlikely to persist in disturbed habitats (Pimm and Lawton 1977). However, it is likely that dendritic stream networks have sufficient refuges from physical disturbance (e.g., sedimentation) that ensure localised extinctions of mobile larger predators are rare events (Thompson and Townsend 2005). Sediment disturbance may contribute to the loss of benthic 'mesopredators', including small demersal fish (Berkman and Rabeni 1987), and the loss of these highly connected taxa has the potential to shorten FCL (Post and Takimoto 2007, Anderson and Cabana 2009). Moreover, theoretical studies that have addressed how the network structure of a food-web influences species additions and deletions have shown that removing the

most highly connected ones causes more cascading extinctions than does random removal (Dunne et al. 2002).

Strong empirical evidence of dynamic constraints is still lacking however (Takimoto and Post 2012), and is often confounded by effects of disturbance on resource availability (McHugh et al. 2010). Moreover, species replacements along an environmental gradient may be common in aquatic systems thus regulating trophic structure (Leibold et al. 1997), and in lotic habitats, the complete extirpation of highly mobile stream invertebrates in response to physical disturbance may be uncommon (Death and Winterbourn 1995). However, one of the few studies to consider the effects of sedimentation on stream trophic linkages showed that food webs became simpler, with fewer nodes and links, lower linkage density, and lower complexity (Yule et al. 2010). Those researchers measured impacts from a large sediment disturbance on a tropical river, with inputs from alluvial gold mining appearing to be exacerbated by a seasonal low flow event (i.e., ~70% reduction in median base flow) around the time of sampling. Despite the high levels of sediment pollution, fish distribution and diets did not appear to be affected (Yule et al. 2010). It seems likely that although some structural food-web properties may be affected by perturbations (Townsend et al. 1998, Yule et al. 2010), only the most extreme and prolonged sediment disturbance will lead to shorter FCL by drastically decreasing basal production and eliminating entire guilds of higher consumers. This suggests that understanding the shifting interaction strengths contained within food webs in response to perturbations, as opposed to structural changes such as FCL, may be more important to stream ecosystems experiencing disturbance (Woodward and Hildrew 2002).

Sediment influences on trophic interactions

Sedimentation strongly affects community composition, and this may have consequences for the functional dynamics of stream ecosystems by affecting certain trophic pathways (Fig 3a,b). Yule et al. (2010) reported the loss of grazers, shredders, and filter-feeders with a large sediment disturbance in a tropical river. Consumers that graze attached algae on rocks are sensitive to deposited sediment, and the feeding activities and energy derived by these organisms may be inhibited by lower periphyton quality and quantity and/or reduced access to food resources (Berkman and Rabeni 1987, Rabení et al. 2005). Similarly, filter-feeders perform an important role as integrators of seston into benthic production (Malmqvist et al. 2001), but may be susceptible to the effects of sediment entrainment and deposition due to their feeding behaviour and generally sedentary nature (Box and Mossa 1999, Runde and Hellenthal 2000, Connolly and Pearson 2007).

In contrast, organisms feeding on buried particulate matter and micro-organisms associated with fine sediments may benefit from sedimentation (Fig 3b). Numerous studies have documented increases in organisms that filter food resources from the surrounding sediment such as sphaerid clams (Lopez and Holopainen 1987) and burrowing deposit-feeders (e.g., oligochaetes, nematodes, and Chironomini midge larvae) in response to increased sediment deposition (Waters 1995, Matthaei et al. 2006, Larsen et al. 2010). The increase in deposit-feeders can be a response to increased availability of fine benthic organic matter and associated heterotrophs (Nuttall 1972, Winterbourn 2000). These changes can force polyphagous grazers to become facultative collectors at sites with excessive deposited sediment (Yule et al. 2010). However, pulsed sediment disturbance may still affect these trophic pathways (Matthaei et al. 2006), and food resource availability can strongly influence abundances (Syrovatka et al. 2009).

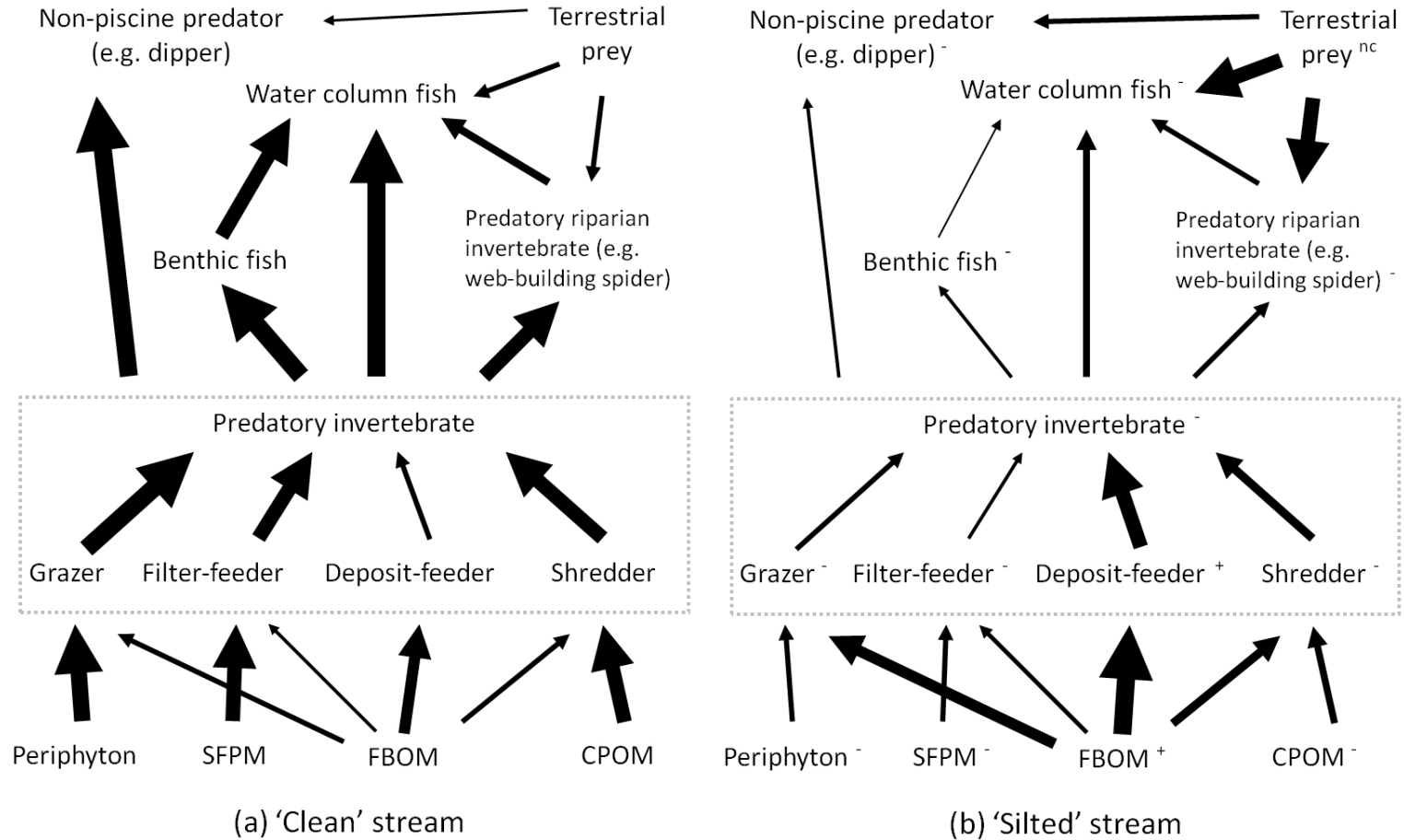


FIG. 3. Simplified food-web diagram showing energy flow through functional-feeding groups in (a) a 'clean' stream with low levels of fine inorganic sediment and (b) a 'silted' stream with high levels of deposited sediment. Invertebrate feeding groups have been compartmentalized for simplicity (see inset box). Groupings are not mutually exclusive (e.g., collectors). Thickness of lines indicates the magnitude of energy flow. Positive and negative signs indicate net direction of sediment effects on food web groups (nc = no change). CPOM, coarse particulate organic matter; FBOM, Fine benthic organic matter; SFPM, suspended fine particulate matter.

Although it has been suggested that sediment impacts are less in detrital-based streams (Ryan 1991), sediment may reduce the availability and quality of allochthonous resources to ‘shredding’ detritivores, thus affecting rates of detrital processing (Sponseller and Benfield 2001, Navel et al. 2010). Despite the ubiquity of sediment impacts in streams affected by human land-use activities and the importance of the detrital pathway to stream ecosystems, sediment influences on litter decomposition remains poorly understood, and the results that have been reported in the literature are often equivocal (Sponseller and Benfield 2001, Niyogi et al. 2003). Overall however, these studies suggest a greater reliance on heterotrophic food resources in streams affected by sediment, and a reduction in more specialised consumers; particularly those that acquire energy from grazing periphyton or filtering resources from the water column (Fig 3b). However, the potential consequences of reduced trophic diversity (i.e., simpler food webs) in response to sedimentation remain poorly understood, but suggests that ecosystem functions such as biomass production and detrital processing may be impaired. These changes may also undermine ecosystem stability, if sedimentation leads to structural asymmetry in the energetic pathways of food webs (Rooney et al. 2006). However, in systems where resource availability is low, generalist feeding (polyphagy and trophic omnivory) may be advantageous leading to highly interconnected food webs (Woodward and Hildrew 2002).

In some instances, the reduction of habitat complexity may increase predation risk for prey by removing refugia. Prey vulnerability to predators is important in determining trophic interactions (Power et al. 1992), and predation rates of benthic fish on vulnerable insect prey were increased where additions of sediment reduced interstitial refugia (Brusven and Rose 1981). Sediment-induced loss of refugia in experimental stream channels reduced the abundance of upland bullies (*Gobiomorphus breviceps*) by 60% through emigration (Jowett and Boustead

2001), and reduced benthic cover can intensify predation on demersal fish (White and Harvey 2001). More generally, however, the reduction of prey by sediment may alter consumptive interactions and reduce the flow of energy through stream food webs (Fig. 3b).

Sedimentation can reduce invertebrate biomass (Angradi 1999), and the reduction of prey may offset consumptive effects by predators (Peckarsky 1984, Schofield et al. 2004). Numerous studies have documented decreases in predatory fish biomass and abundance as benthic invertebrate composition changes with sedimentation (Waters 1982, Alexander and Hansen 1986, Mol and Ouboter 2004). Shifts in invertebrate communities from vulnerable taxa to burrowing and armoured forms across an experimental sediment gradient led to a concomitant decline in predator growth and survival rates (Suttle et al. 2004). Moreover, the "size disparity" hypothesis suggests that there are lower limits on the body size of consumable prey for predators, meaning that body size constraints can lead to strong food-web compartmentalization (Schmid-Araya et al. 2002). This may be particularly relevant to stream food webs affected by sediment, if smaller-bodied invertebrate communities are associated with habitat dominated by fine-grained substrates (Palmer 1990, Bourassa and Morin 1995, Gayraud and Phillippe 2001). Where suspended sediment contributes to increased turbidity, visual-feeding by predatory fish may be affected (Shaw and Richardson 2001).

Changes in prey availability induced by sediment may not only affect predatory fish. The dipper (Cinclidae: *Cinclus* spp.) found in the Americas and Eurasia is a passerine river specialist strongly influenced by habitat quality (Buckton and Ormerod 2002, Larsen et al. 2010). Feck and Hall (2004) found a strong correlation between the abundance of the American dipper (*Cinclus mexicanus*) and its sediment-sensitive invertebrate prey. In New Zealand, a natural disturbance caused excessive inputs of sediment to a river, thus reducing prey quantity and quality, and

potentially influencing a decline in the population density and fecundity of whio (*Anatidae: Hymenolaimus malacorrhynchos*), an endemic river specialist that fills a similar niche to the dipper (Collier 2004). These studies suggest sediment may contribute to reduced prey availability and concomitant effects on non-piscine stream predators (Fig. 3b).

Sediment and cross-habitat interactions

The effects of sediment pollution may propagate across traditional habitat boundaries (Fig. 3b). Sediment may reduce the abundance of emergent aquatic insects, thus dampening the export of prey subsidies to terrestrial consumers including riparian spiders (Laeser et al. 2005, Burdon and Harding 2008). Wagner (1984) showed that excessive sediment covering a stream reach strongly reduced emergent insect abundance and biomass; manipulative studies that similarly reduced emergent prey led to decreased abundances of riparian spiders (e.g., Marczak and Richardson 2007). Growth rates and maximal body size may also be impaired (Akamatsu et al. 2007), which could restrict the ability of riparian spiders to act as integrators of aquatic and terrestrial derived energy (Holt 2006), thus diminishing their potential reciprocal contribution to aquatic food webs as allochthonous prey (Burdon and Harding 2008).

For large mobile predators, resource subsidies of prey from riparian zones and unaffected upstream tributaries (Nakano et al. 1999, Wipfli and Gregovich 2002) may help mitigate the ‘bottom-up’ impacts of sediment on benthic production (Mol and Ouboter 2004, Yule et al. 2010). Assuming predatory fish are generalists that can consume both terrestrial and aquatic prey, allochthony can either exert positive or negative indirect effects upon benthic invertebrates. Positive effects due to ‘prey-switching’ may be driven both by prey characteristics and densities, although ‘apparent competition’ leading to a numerical and/or functional response by predators might cause negative indirect effects on benthic invertebrate prey (Holt 1984, Baxter et al. 2005).

Moreover, where space is limited or homogeneous, the stabilising influence of higher trophic levels can be compromised leading to strong ‘top-down’ suppression, meaning that mobile predators can be destabilizing in spatially constrained ecosystems (McCann et al. 2005, Rooney et al. 2006).

Harsh-benign and environmental stress

Even if the basic food-web structure remains unchanged (e.g., food-chain length), sediment pollution may drive greater ‘top-down’ suppression of vulnerable prey whilst simultaneously causing a ‘bottom-up’ trophic cascade, with the transfer of energy greatly reduced across multiple trophic levels. Stream food webs are generally size-structured, meaning that large organisms tend to occupy higher trophic levels and consumer–resource interactions (e.g., trophic cascades) can often be more important than horizontal interactions, indicating that vertical connections may disproportionately influence stream food-web dynamics (Woodward and Warren 2007, Woodward 2009). This means that interactions such as herbivory and predation can be just as important as species richness for determining ecosystem functioning (Tylianakis et al. 2007, Woodward 2009), and the indirect effects of perturbations mediated through species interactions may outweigh the direct pathways (Menge 1995). The harsh-benign (HB) framework predicts that along a gradient of increasing physical stress, biotic interactions weaken as abiotic factors start to dominate community structure and function (Peckarsky 1983); thus offering a stream ecology perspective to Menge and Sutherland (1976). However, perturbations can strengthen interactions by altering community composition and faunal traits (Wootton et al. 1996, Nystrom and McIntosh 2003, Tylianakis et al. 2007), thus suggesting that allowing for differing tolerances of predators and prey to disturbance may be a more useful theoretical construct than that of HB (Menge and Olson 1990).

Concluding remarks

Sediment pollution is a widespread and pervasive problem affecting streams and rivers globally, and is a major pathway whereby the intensification of agriculture exerts pressure on aquatic habitats. The direct effects of physical stress coupled with the more indirect effects of reduced food and habitat caused by sedimentation may alter growth, recruitment, emigration, and mortality rates of aquatic organisms across multiple trophic levels. Sedimentation may reduce ecosystem productivity, and disproportionately affect autotrophs leading to a shift in the trophic basis of production to heterotrophic pathways. There is evidence to suggest sedimentation impairs detrital processing through direct physical and indirect biological mechanisms. Numerous studies have shown that benthic invertebrate communities change with increasing sedimentation, and shifts in abundances and composition may be abrupt, thus indicating threshold responses to sediment. However, further research is required to better describe these non-linear responses and the underlying mechanisms. Sediment-induced reduction of key species populations within a trophic level may affect the next via diminished transfers of energy, and these effects may propagate across stream boundaries, thus affecting riparian predators and reciprocal linkages of prey. Although food-chain length may be a poor indicator of change, functional-feeding groups that integrate different energetic pathways (e.g., ‘grazers’, ‘filter-feeders’, and ‘shredders’) can be disproportionately affected by sediment. These changes may lead to simpler food webs with distorted interaction strengths and asymmetry in energetic pathways, thus potentially contributing to decreased ecosystem functioning and reduced stability.

Complex synergies, including the strong nexus between flow regimes and in-stream habitat, reinforce the need to better understand how environmental context influences sediment impacts. Although context-dependent effects may reflect the influence of topography and

catchment geology, the predicted climate change driving fluctuations in rainfall patterns and more frequent extreme weather events is expected to exert stress on lotic communities through direct and indirect pathways (IPCC 2001, Woodward et al. 2010). Although increased sediment flux and retention is likely to be a significant corollary of climate change, this indirect pathway has been given little attention in the recent literature investigating the potential ramifications for freshwater ecosystems. In regions dominated by agriculture, the changing spatial and temporal distribution of precipitation, coupled with increased demand for water resources and the intensity of farming practices will likely have synergistic effects on anthropogenic stressors in freshwaters (Heathwaite 2010). Addressing these challenges will require scientists to collaborate across multiple disciplines. Nevertheless, recognising how sediment affects lotic communities across multiple levels of biological organisation, along with robustly quantifying impact thresholds, is critical in a changing world if we are to preserve biodiversity and ecosystem function.

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LITERATURE CITED

Akamatsu, F., H. Toda, and T. Okino. 2007. Relating body size to the role of aquatic subsidies for the riparian spider *Nephila clavata*. *Ecological Research* 22:831-836.

- Aldridge, D. W., B. S. Payne, and A. C. Miller. 1987. The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. *Environmental Pollution* 45:17-28.
- Alexander, G. R., and E. A. Hansen. 1986. Sand bed load in a brook trout stream. *North American Journal of Fisheries and Management* 6:9-23.
- Allan, D. J. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257-284.
- Allan, D. J., D. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37:149-161.
- Anderson, C., and G. Cabana. 2009. Anthropogenic alterations of lotic food web structure: evidence from the use of nitrogen isotopes. *Oikos* 118:1929-1939.
- Angradi, T. R. 1999. Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society* 18:49-66.
- Armour, C. L., D. A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. *Fisheries* 16:7-11.
- Atkinson, B. L., M. R. Grace, B. T. Hart, and K. Vanderkruk. 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201-220.

- Benoy, G. A., A. B. Sutherland, J. M. Culp, and R. B. Brua. 2012. Physical and ecological thresholds for deposited sediments in streams in agricultural landscapes. *Journal of Environmental Quality* 41:31-40.
- Berkman, H., and C. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285-294.
- Biggs, B. J. F. 2000. New Zealand periphyton guideline: detecting, monitoring and managing enrichment of streams. Ministry for the Environment, Wellington, NZ.
- Boubee, J. A. T., T. L. Dean, D. W. West, and R. F. G. Barrier. 1997. Avoidance of suspended sediment by the juvenile migratory stage of six New Zealand native fish species. *New Zealand Journal of Marine and Freshwater Research* 31:61-69.
- Bourassa, N., and A. Morin. 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *Journal of the North American Benthological Society* 14:393-403.
- Box, J. B., and J. Mossa. 1999. Sediment, land use, and freshwater mussels: prospects and problems. *Journal of the North American Benthological Society* 18:99-117.
- Brunke, M., and T. Gonser. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37:1-33.
- Brusven, M. A., and S. T. Rose. 1981. Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin, *Cottus rhotheus*. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1444-1448.
- Bryce, S. A., G. A. Lomnický, and P. R. Kaufmann. 2010. Protecting sediment sensitive aquatic species in mountain streams through the application of biologically based criteria

- streambed sediment criteria. *Journal of the North American Benthological Society* 29:657–672.
- Buckton, S. T., and S. J. Ormerod. 2002. Global patterns of diversity among the specialist birds of riverine landscapes. *Freshwater Biology* 47:695-709.
- Burdon, F. J., and J. S. Harding. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology* 53:330-346.
- Cairns, J., Jr. 1977. Aquatic ecosystem assimilative capacity. *Fisheries* 2:5-7.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264–270.
- Cline, L. D., R. A. Short, and J. V. Ward. 1982. The influence of highway construction on the macroinvertebrates and epilithic algae of a high mountain stream. *Hydrobiologia* 96:149-159.
- Collier, K. J. 2004. Perturbation pathways affecting the avian lotic predator, blue duck, following a volcanic eruption. *Freshwater Biology* 49:818-834.
- Collier, K. J., and J. M. Quinn. 2003. Land-use influences macroinvertebrate community response following a pulse disturbance. *Freshwater Biology* 48:1462-1481.
- Connolly, N., and R. Pearson. 2007. The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flow-through artificial stream channels and recirculating mesocosms. *Hydrobiologia* 592:423-438.
- Cordone, A. J., and D. W. Kelly. 1961. The influences of inorganic sediment on the aquatic life of streams. *California Fish and Game* 47:189-228.

- Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64:1345-1351.
- Davies-Colley, R., C. W. Hickey, J. M. Quinn, and P. A. Ryan. 1992. Effects of clay discharges on streams: 1. Optical properties and epilithon. *Hydrobiologia* 248:215-234.
- Death, R. G., B. Baillie, and P. Fransen. 2003. Effect of *Pinus radiata* logging on stream invertebrate communities in Hawke's Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 37:507-520.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76:1446-1460.
- Dickman, M. D., M. R. Peart, and W. W. S. Yim. 2005. Benthic diatoms as indicators of stream sediment concentration in Hong Kong. *International Review of Hydrobiology* 90:412-421.
- Donohue, I., and J. G. Molinos. 2009. Impacts of increased sediment loads on the ecology of lakes. *Biological Reviews* 9999.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163-182.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558-567.
- Feck, J., and R. O. Hall. 2004. Response of American dippers (*Cinclus mexicanus*) to variation in stream water quality. *Freshwater Biology* 49:1123-1137.

- Folt, C. L., C. Y. Chen, M. V. Moore, and J. Burnaford. 1999. Synergism and antagonism among multiple stressors. *Limnology and Oceanography* 44:864-877.
- Francoeur, S. N., and B. J. F. Biggs. 2006. Short-term effects of elevated velocity and sediment abrasion on benthic algal communities. *Hydrobiologia* 561:59-69.
- Gayraud, S., and M. Phillippe. 2001. Does subsurface interstitial space influence general features and morphological traits of the benthic macroinvertebrate community in streams? *Archiv für Hydrobiologie* 151:667-686
- Gordon, N. D., T. A. McMahon, B. L. Finlayson, and R. J. Nathan. 2004. Stream hydrology: an introduction for ecologists. John Wiley & Sons Ltd, Chicester, England, UK.
- Graham, A. A. 1990. Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspension. *Hydrobiologia* 199:107-115.
- Gücker, B., I. G. Boechat, and A. Giani. 2009. Impacts of agricultural land use on ecosystem structure and whole-stream metabolism of tropical Cerrado streams. *Freshwater Biology* 54:2069-2085.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95:14843-14847.
- Harrison, S. S. C., J. L. Pretty, D. Shepherd, A. G. Hildrew, C. Smith, and R. D. Hey. 2004. The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology* 41:1140-1154.
- Heathwaite, A. L. 2010. Multiple stressors on water availability at global to catchment scales: understanding human impact on nutrient cycles to protect water quality and water availability in the long term. *Freshwater Biology* 55:241-257.

- Herbert, D. W. M., and J. C. Merckens. 1961. The effect of suspended mineral solids on the survival of trout. *International Journal of Air and Water Pollution* 5:46-55.
- Herbst, D. B., M. T. Bogan, S. K. Roll, and H. D. Safford. 2012. Effects of livestock exclusion on in-stream habitat and benthic invertebrate assemblages in montane streams. *Freshwater Biology* 57:204-217.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *The American Naturalist* 124:377.
- Holt, R. D. 2006. Ecology: asymmetry and stability. *Nature* 442:252-253.
- Homan, R. N., B. S. Windmiller, and J. M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14:1547-1553.
- IPCC. 2001. *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, UK.
- Jensen, D. W., E. A. Steel, A. H. Fullerton, and G. R. Pess. 2009. Impact of fine sediment on egg-to-fry survival of Pacific Salmon: A meta-analysis of published studies. *Reviews in Fisheries Science* 17:348-359.
- Jessup, B. K., D. Eib, L. Guevara, J. Hogan, F. John, S. Joseph, P. Kaufmann, and A. Kosfiszer. 2010. *Sediment in New Mexico streams: existing conditions and potential benchmarks*. Report prepared for the U.S. Environmental Protection Agency, Region 6, Dallas, TX and the New Mexico Environment Department, Santa Fe, NM. Prepared by Tetra Tech, Inc., Montpelier, VT, USA.

- Jones, E. B. D., G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology* 13:1454-1465.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055-1071.
- Jowett, I. G., and N. C. Boustead. 2001. Effects of substrate and sedimentation on the abundance of upland bullies (*Gobiomorphus breviceps*). *New Zealand Journal of Marine and Freshwater Research* 35:605-613.
- Kemp, P., D. Sear, A. Collins, P. Naden, and I. Jones. 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes* 25:1800-1821.
- Kent, T., and R. Stelzer. 2008. Effects of deposited fine sediment on life history traits of *Physa integra* snails. *Hydrobiologia* 596:329-340.
- Laeser, S., C. Baxter, and K. Fausch. 2005. Riparian vegetation loss, stream channelization, and web-weaving spiders in northern Japan. *Ecological Research* 20:646-651.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573-592.
- Larsen, S., and S. J. Ormerod. 2009. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology* 55:476-486.
- Larsen, S., G. Pace, and S. J. Ormerod. 2010. Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams. *River Research and Applications* 27:257-267.

- Larsen, S., A. Sorace, and L. Mancini. 2010. Riparian bird communities as indicators of human impacts along Mediterranean streams. *Environmental Management* 45:261-273.
- Larsen, S., I. P. Vaughan, and S. J. Ormerod. 2009. Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biology* 54:203-219.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467-494.
- Lemly, A. 1982. Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* 87:229-245.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.
- Lopez, G. R., and I. J. Holopainen. 1987. Interstitial suspension feeding by *Pisidium* spp. (Pisidiidae: Bivalvia): a new guild in the lentic benthos? *American Malacological Bulletin* 5:21-30.
- Malmqvist, B., R. S. Wotton, and Y. Zhang. 2001. Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos* 92:35-43.
- Marczak, L. B., and J. S. Richardson. 2007. Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology* 76:687-694.
- Matthaei, C. D., J. J. Piggott, and C. R. Townsend. 2010. Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology* 47:639-649.
- Matthaei, C. D., F. Weller, D. W. Kelly, and C. R. Townsend. 2006. Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology* 51:2154-2172.

- McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. *Ecology Letters* 8:513-523.
- McHugh, P. A., A. R. McIntosh, and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters* 13:881-890.
- McTammany, M. E., E. F. Benfield, and J. R. Webster. 2008. Effects of agriculture on wood breakdown and microbial biofilm respiration in southern Appalachian streams. *Freshwater Biology* 53:842-854.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21-54.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology & Evolution* 5:52-57.
- Menge, B. A., and J. P. Sutherland. 1976. Species-diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. *The American Naturalist* 110:351-369.
- Mol, J. H., and P. E. Ouboter. 2004. Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small neotropical rainforest stream. *Conservation Biology* 18:201-214.
- Molinos, J. G., and I. Donohue. 2009. Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society* 28:110-121.
- Molinos, J. G., and I. Donohue. 2011. Temporal variability within disturbance events regulates their effects on natural communities. *Oecologia* 166:795-806.

- Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80:2435-2441.
- Navel, S., F. Mermillod-Blondin, B. Montuelle, E. Chauvet, L. Simon, C. Piscart, and P. Marmonier. 2010. Interactions between fauna and sediment control the breakdown of plant matter in river sediments. *Freshwater Biology* 55:753-766.
- Newman, M. 2011. Molecular phylogenetic characterization of microbial community dynamics associated with freshwater stream environmental organic matter sources. Ph.D thesis. Department of Biological Sciences, University of Auburn, Alabama, USA.
- Niyogi, D. K., K. S. Simon, and C. R. Townsend. 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology* 48:1698-1708.
- Nuttall, P. M. 1972. The effects of sand deposition upon the macroinvertebrate fauna of the River Camel, Cornwall. *Freshwater Biology* 2:181-186.
- Nystrom, P., and A. R. McIntosh. 2003. Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia* 136:279-288.
- Osmundson, D. B., R. J. Ryel, V. L. Lamarra, and J. Pitlick. 2002. Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. *Ecological Applications* 12:1719-1739.
- Palmer, M. A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *Journal of the North American Benthological Society* 9:17-25.
- Pardini, R., A. d. A. Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE* 5:e13666.

- Pascoal, C., F. Cássio, A. Marcotegui, B. Sanz, and P. Gomes. 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. *Journal of the North American Benthological Society* 24:784-797.
- Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of community structure. Pgs 303-324 *in* Dynamics of Lotic Ecosystems. T. D. Fontaine and S. M. Bartell (eds.). Ann Arbor Science Publishers Ann Arbor, MI, USA.
- Peckarsky, B. L. 1984. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology* 63:1519-1530.
- Peeters, E., B. Brugmans, J. Beijer, and R. Franken. 2006. Effect of silt, water and periphyton quality on survival and growth of the mayfly *Heptagenia Sulphurea*. *Aquatic Ecology* 40:373-380.
- Petchey, O. L., A. L. Downing, G. G. Mittelbach, L. Persson, C. F. Steiner, P. H. Warren, and G. Woodward. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467-478.
- Pimentel, D., J. Allen, A. Beers, L. Guinand, R. Linder, P. McLaughlin, B. Meer, D. Musonda, D. Perdue, S. Poisson, S. Siebert, K. Stoner, R. Salazar, and A. Hawkins. 1987. World agriculture and soil erosion. *BioScience* 37:277-283.
- Pimentel, D., B. Berger, D. Filiberto, M. Newton, B. Wolfe, E. Karabinakis, S. Clark, E. Poon, E. Abbett, and S. Nandagopal. 2004. Water resources: agricultural and environmental issues. *BioScience* 54:909-918.
- Pimm, S. L. 1982. Food webs. Chapman and Hall, New York, USA.
- Pimm, S. L., and J. H. Lawton. 1977. Number of trophic levels in ecological communities. *Nature* 268:329-331.

- Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution* 17:269-277
- Post, D. M., and G. Takimoto. 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116:775-782.
- Power, M. E., J. C. Marks, and M. S. Parker. 1992. Variation in the vulnerability of prey to different predators - community-level consequences. *Ecology* 73:2218-2223.
- Quinn, J., and C. W. Hickey. 1990. Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* 24:387-409
- Rabeni, C., K. Doisy, and L. Zweig. 2005. Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences* 67:395-402.
- Relyea, C. D., G. W. Minshall, and R. J. Danehy 2000. Stream insects as bioindicators of fine sediment. Pgs 663-686 in *Proceedings of the Water Environment Federation Watershed Management 2000 Conference*. Water Environment Federation, Alexandria, VA, USA.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- Richards, C., and K. L. Bacon. 1994. Influence of fine sedimentation on macroinvertebrate colonisation of surface and hyporheic stream substrates. *Great Basin Naturalist* 54:106-113.
- Rier, S. T., and D. K. King. 1996. Effects of inorganic sedimentation and riparian clearing on benthic community metabolism in an agriculturally-disturbed stream. *Hydrobiologia* 339:111-121.

- Romani, A. M., and S. Sabater. 2001. Structure and activity of rock and sand biofilms in a Mediterranean stream. *Ecology* 82:3232-3245.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265-269.
- Rowe, D. K., and T. L. Dean. 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research* 32:21-29.
- Runde, J. M., and R. A. Hellenthal. 2000. Behavioral responses of *Hydropsyche sparna* (Trichoptera: Hydropsychidae) and related species to deposited bedload sediment. *Environmental Entomology* 29:704-709.
- Ryan, P. A. 1991. Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* 25:207-221.
- Ryder, G. I. 1989. Experimental studies on the effects of fine sediments on lotic invertebrates. Ph.D. thesis. Department of Zoology, University of Otago, Dunedin, NZ.
- Sanpera-Calbet, I., E. Chauvet, and J. Richardson. 2012. Fine sediment on leaves: shredder removal of sediment does not enhance fungal colonisation. *Aquatic Sciences* 74:527-538.
- Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591-596.
- Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution* 8:275-279.
- Schmid-Araya, J. M., P. E. Schmid, A. Robertson, J. Winterbottom, C. Gjerløv, and A. G. Hildrew. 2002. Connectance in stream food webs. *Journal of Animal Ecology* 71:1056-1062.

- Schofield, K. A., C. M. Pringle, and J. L. Meyer. 2004. Effects of increased bedload on algal- and detrital-based stream food webs: Experimental manipulation of sediment and macroconsumers. *Limnology and Oceanography* 49:900-909.
- Scrimgeour, G. J., R. J. Davidson, and J. M. Davidson. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 22:337-344.
- Shaw, E. A., and J. S. Richardson. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2213-2221.
- Smith, V. H., G. D. Tilman, and J. C. Nekola. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* 100:179-196.
- Sponseller, R. A., and E. F. Benfield. 2001. Influences of land use on leaf breakdown in Southern Appalachian headwater streams: a multiple-scale analysis. *Journal of the North American Benthological Society* 20:44-59.
- Sponseller, R. A., E. F. Benfield, and H. M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409-1424.
- Suren, A. M. 2005. Effects of deposited sediment on patch selection by two grazing stream invertebrates. *Hydrobiologia* 549:205-218.
- Sutherland, A. B., J. L. Meyer, and E. P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47:1791-1805.

- Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* 14:969-974.
- Syrovatka, V., J. Schenkova, and K. Brabec. 2009. The distribution of chironomid larvae and oligochaetes within a stony-bottomed river stretch: the role of substrate and hydraulic characteristics. *Fundamental and Applied Limnology* 174:43-62.
- Takimoto, G., and D. M. Post. 2012. Environmental determinants of food-chain length: a meta-analysis. *Ecological Research* doi:10.1007/s11284-012-0943-7.
- Thompson, R. M., J. A. Dunne, and G. Woodward. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology* 57:1329-1341.
- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137-148.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.
- Townsend, C. R., R. M. Thompson, A. McIntosh, C. Kilroy, E. Edwards, and M. Scarsbrook. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters* 1:200-209.
- Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202-205.
- Vasconcelos, M. D., and A. S. Melo. 2008. An experimental test of the effects of inorganic sediment addition on benthic macroinvertebrates of a subtropical stream. *Hydrobiologia* 610:321-329.

- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Wagenhoff, A., C. R. Townsend, and C. D. Matthaei. 2012. Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology* 49:892-902.
- Wagner, R. 1984. Effects of an artificially changed stream bottom on emerging insects. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22:2042-2047.
- Wallace, B. J., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104.
- Walling, D. E. 1990. Linking the field to the river: Sediment delivery from agricultural land. Pgs 129-152 *in* Soil erosion on agricultural land. J. Boardman, I. D. L. Foster and J. A. Dearing (eds.). John Wiley, Chichester, UK.
- Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2-8.
- Waters, T. F. 1982. Annual production by a stream brook charr population and by its principal invertebrate food. *Environmental Biology of Fishes* 7:165-170.
- Waters, T. F. 1995. Sediment in streams. sources, biological effects, and control. American Fisheries Society, Bethesda, Maryland, USA.
- White, J. L., and B. C. Harvey. 2001. Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. *Freshwater Biology* 46:987-995.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

- Winterbourn, M. J. 2000. Feeding ecology. Pgs 100-124 *in* New Zealand stream invertebrates: ecology and implications for management. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. *Freshwater Biology* 47:957-969.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21:203-217.
- Wood, P. J., and P. D. Armitage. 1999. Sediment deposition in a small lowland stream: management implications. *Regulated Rivers: Research and Management* 15:199-210.
- Wood, P. J., J. Toone, M. T. Greenwood, and P. D. Armitage. 2005. The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv für Hydrobiologie* 163:145-162.
- Woodward, G. 2009. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology* 54:2171-2187.
- Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2093-2106.
- Woodward, G., and P. Warren 2007. Body size and predatory interactions in freshwaters: scaling from individuals to communities Pgs 98-117 *in* Body size: the structure and function of aquatic ecosystems. A. G. Hildrew, D. G. Raffaelli and R. Edmonds-Brown (eds.). Cambridge University Press, Cambridge, UK.
- Woodward, G. U. Y., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. *Freshwater Biology* 47:777-798.

- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558-1561.
- Yamada, H., and F. Nakamura. 2002. Effect of fine sediment deposition and channel works on periphyton biomass in the Makomanai River, northern Japan. *River Research and Applications* 18:481-493.
- Yule, C. M., L. Boyero, and R. Marchant. 2010. Effects of sediment pollution on food webs in a tropical river (Borneo, Indonesia). *Marine and Freshwater Research* 61:204-213.
- Zimmerman, J. K. H., B. Vondracek, and J. Westra. 2003. Agricultural land use effects on sediment loading and fish assemblages in two Minnesota (USA) watersheds. *Environmental Management* 32:93-105.

CHAPTER 2: PREAMBLE

Chapter 2 focuses on the question posed in Chapter 1: Are there structural changes to stream communities in response to sedimentation?, but seeks to further our understanding of sediment impacts by investigating threshold biotic responses. Numerous studies have identified changes in invertebrate community composition in response to sedimentation (Jones et al. 2012). However, in Chapter 1, the potential for non-linear (e.g., threshold) responses to sediment deposition by stream invertebrate communities were reviewed, with known values from previous studies summarized. These threshold responses can reflect an abrupt shift in community structure, and typically involve a change from an assemblage dominated by EPT taxa (sediment-sensitive insect orders Ephemeroptera, Plecoptera, Trichoptera) to one characterized by worms, snails, and micro-crustaceans (Waters 1995). Less well understood, however, are the underlying mechanisms driving such changes, and how spatial context influences sediment thresholds. Thus, Chapter 2 builds on the knowledge gaps identified in the literature review (Chapter 1) and investigates threshold responses and the potential underlying mechanisms influencing these non-linear changes in community structure. To do this, I surveyed 30 streams on the Canterbury Plains along gradients of deposited sediment and dissolved nutrients (e.g., nitrate).

LITERATURE CITED

- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055-1071.
- Waters, T. F. 1995. Sediment in streams. sources, biological effects, and control. American Fisheries Society, Bethesda, Maryland, USA.

CHAPTER 2

HABITAT LOSS DRIVES THRESHOLD RESPONSE OF BENTHIC INVERTEBRATE

COMMUNITIES TO DEPOSITED SEDIMENT IN AGRICULTURAL STREAMS



A stream badly affected by sedimentation near Lincoln, Canterbury Plains

Abstract. Agricultural land uses can impact stream ecosystems by reducing suitable habitat, altering flows, and increasing inputs of diffuse pollutants including fine inorganic sediment (<2 mm). These changes have been linked to altered community composition and declines in biodiversity. Determining the mechanisms driving stream biotic responses, particularly threshold impacts, has, however, proved elusive. To investigate a sediment threshold response by benthic invertebrates, an intensive survey of 30 agricultural streams was conducted along gradients of deposited sediment and dissolved nutrients. Partial redundancy analysis showed that invertebrate community composition changed significantly along the gradient of deposited fine sediment, whereas the effect of dissolved nitrate was weak. Pollution-sensitive invertebrates (% EPT, Ephemeroptera, Plecoptera, Trichoptera) demonstrated a strong non-linear response to sediment, and change-point analysis indicated marked declines beyond a threshold of approximately 20% fine sediment covering the streambed. Structural equation modeling indicated that decreased habitat availability (i.e., coarse substrate and associated interstices) was the key driver affecting pollution-sensitive invertebrates, with degraded riparian condition controlling resources through direct (e.g., inputs) and indirect (e.g., flow-mediated) effects on deposited sediment. The identification of specific effects thresholds and the underlying mechanisms (e.g., loss of habitat) driving these changes will assist managers in setting sediment criteria and standards to better guide stream monitoring and rehabilitation.

Keywords: diffuse pollution; fine inorganic sediment; global change; nitrate; non-linear response; riparian management; sedimentation; stream invertebrate communities; threshold impact.

INTRODUCTION

Agriculture is the dominant form of human land use globally, occupying the largest proportion of area in many developed catchments (Allan 2004). Furthermore, as the world's population increases, agriculture will need to become more intensive (Vitousek et al. 1997). Consequently, demands for increased yields are predicted to cause unprecedented ecosystem simplification, loss of ecosystem services, and species extinctions (Tilman et al. 2001). Moreover, changes to habitat leading to altered species distributions may influence biotic interactions, with deleterious consequences for ecosystem functioning and food web stability (Tylianakis et al. 2007).

Numerous studies have documented declines in water and habitat quality, and changes in aquatic community structure and richness, in association with agricultural expansion and intensification (Allan et al. 1997, Harding et al. 1999, Sponseller et al. 2001). Agricultural land uses impact streams by changing riparian and channel habitat, reducing bank stability, altering flows, and increasing diffuse inputs of pollutants including fine inorganic sediment and nutrients (Allan 2004). In particular, increased stream sedimentation has often been associated with non-point sources arising from agricultural land uses (Walling 1990). Overgrazing of riparian zones and surrounding uplands (Armour et al. 1991, Fleischner 1994, Braccia and Voshell 2007) is generally associated with negative influences on benthic invertebrate community composition and other indicators of stream health (Harding et al. 1999). However, an incomplete understanding of the mechanisms underlying these effects and associated thresholds has made it difficult to manage ongoing issues.

Sediment is recognized as a leading cause of biological impairment in rivers and streams of many countries (USEPA 2000). Declines in taxa richness and altered community composition

with increased sediment deposition, thus leading to reduced abundances of sediment-sensitive biota (% EPT, Ephemeroptera, Plecoptera, Trichoptera), are well documented (Berkman and Rabeni 1987, Angradi 1999, Larsen et al. 2009). This has led researchers to propose threshold responses to deposited sediment (Bryce et al. 2010). Despite this, difficulties of measuring this stressor have hampered efforts to identify reliable thresholds of impact upon stream biota including benthic invertebrate communities (Benoy et al. 2012). Non-linear ecological responses to anthropogenic forcing are likely to be common (Dodds et al. 2010), and combined stressor effects may result in strengthening non-linear relationships (Baldy et al. 2007). However, identifying specific thresholds of sediment impact on stream communities is likely to be complicated by multiple perturbation pathways associated with agricultural land uses, including nutrient enrichment (Townsend et al. 2008, Maloney and Weller 2010).

We assessed the effects of two common agricultural stream stressors (deposited fine sediment and dissolved nutrients) on benthic invertebrate communities. We hypothesized that fine sediment would be the more pervasive stressor affecting community composition, and stream assemblages would demonstrate a threshold response to deposited sediment through reduced abundances of sediment-sensitive invertebrates (% EPT). Moreover, we investigated the underlying mechanisms driving these changes to better provide guidance for management. We hypothesized that the relative abundance of sediment-sensitive invertebrates (% EPT) would be more strongly associated with the availability of benthic habitat (coarse substrate and associated interstices) than food resources, and elevated levels of deposited sediment associated with changes to invertebrate communities could be explained partly by degraded riparian condition.

METHODS

Study sites

We studied streams on the Canterbury Plains, located on the eastern side of New Zealand's South Island (Appendix A). Prior to human settlement, the plains comprised a mosaic of forest, shrublands, and wetlands traversed by braided rivers (Wardle 1991), but European settlement of the plains has seen continuous arable production (pasture, livestock, and cropping) become dominant (Haynes and Francis 1990). In the past three decades, widespread conversion to production-driven dairy farming has contributed to intensification of agriculture on the Canterbury Plains (MacLeod and Moller 2006). For example, farmland used for dairying in Canterbury increased by almost 850% between 1980 and 2009 (Pangborn and Woodford 2011). The dominant vegetation types on the plains are pasture (introduced grasses and *Trifolium* spp.) and monocultures of crops, interspersed with windbreaks and hedgerows of introduced conifers (*Cupressus* and *Pinus* spp.), and members of the Salicaceae including poplars (*Populus* spp.) and willows (*Salix* spp.). These vegetation types also form the principal forms of riparian plantings.

Thirty first to third order perennial streams were selected into nine categories of dissolved nutrients and deposited sediment (i.e., a 3×3 factorial design incorporating low, medium, and high levels of nutrients and sediment). Full orthogonality was not realized (e.g., an extra site was added to each of the three sediment categories). To select these initial groups, nutrient status was determined from 'spot' measures of specific conductivity (YSI 63, YSI Incorporated, Yellow Springs, OH, USA), given that specific conductivity is highly correlated with total nitrate concentrations in our study region (Greenwood et al. 2012). Nutrient status in streams was categorized as 'low' ($<110 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$), 'medium' ($110\text{-}200 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$), and 'high' ($>200 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$). These categories represented median nitrate concentrations of 'low' (0.19 mg/L, range 0.03

– 1.82 mg/L), ‘medium’ (2.28 mg/L, range 0.51 – 5.38 mg/L), and ‘high’ (6.03 mg/L, 5.39 – 8.79 mg/L). Fine inorganic sediment (<2 mm in diameter) deposited on the streambed was categorized as ‘low’ (<15%), ‘medium’ (15-50%), and ‘high’ (> 50%) cover. Sediment assessment protocols suggest that bankside estimates of cover made visually are strongly correlated to physical measures of deposited fine inorganic sediment (Clapcott et al. 2011). Site locations and selected physico-chemical variables are summarized in Appendix A. All stream reaches (30 m for instream habitat assessment, 100 m for riparian condition assessment) comprised of run-riffle sequences (pool habitat <2.5% of total channel area), with submerged macrophytes cover not exceeding 40%. Reaches were on separate tributaries (i.e., not located downstream of another) and were sampled on a single occasion between November 2009 and January 2010. This was justified owing to the climatically unpredictable nature of stream environments in New Zealand, which show low levels of seasonality (Winterbourn et al. 1981).

Data collection

In each reach, mean depth and flow velocity (Marsh-McBirney Flo-Mate Model 2000, Hach, Loveland, CO, USA) were calculated from measurements at ten equidistant points across three transects. Spot measurements were made of pH/specific conductivity (YSI 63), dissolved oxygen (% saturation), and temperature (YSI 550A). All water samples for chemical analysis were collected mid-morning, and consisted of filtered (LabServ[®], Thermo Fisher Scientific New Zealand Ltd, North Shore City, NZ, GF/F, 25 mm diameter) stream water (100 ml) collected in opaque acid-washed bottles, which were placed on ice, and then later frozen prior to analysis. Samples were analyzed for nitrate (nitrate and nitrite nitrogen; mg/L; Appendix B.1) and DRP (dissolved reactive phosphorus; µg/L) using a SYSTEAs Easychem discrete colorimetric auto-analyzer (SYSTEAs S.p.A., Anagni, Italy). Ammonia concentrations were not analyzed as

previous research in these streams has shown ammonia levels to be very low (Greenwood et al. 2012). Nitrate was analyzed using the cadmium reduction method and DRP using the molybdate reduction method (APHA 1995). A further 1 L water sample was collected from each site for estimation of total suspended solids (g/L), refrigerated upon return to the laboratory, and processed within 48 hours of collection by filtering through a pre-ashed, pre-weighed glass fibre filter (LabServ® GF/F, 47 mm Ø) prior to drying (50° C, 24 hours), weighing, ashing (550° C, 6 hours), and re-weighing.

Substrate composition and fine sediment were characterized at two different spatial scales (reach and patch) using multiple subjective (visual) and quantitative (physical) measures. ‘Reach’ was the 30 m stream length, whereas a ‘patch’ was the area of the Surber sampler (0.0625 m²) used to collect quantitative invertebrate samples. To quantify sediment cover (and substrate composition) within each ‘reach’, ten 0.09 m² quadrats were selected within the stream reach in a stratified-random manner (Niyogi et al. 2007); substrate composition was assessed visually. Two methods were used to assess substrate composition within a gridded quadrat placed upon the streambed. Using a glass viewing-window, the dominant substrate at 25 points using the grid intersections was recorded, whereas the second method characterized the dominant substrate within each of 16 grids. Substrate class assessment was based on the Wentworth scale (Wentworth 1922). These methods were repeated at each ‘patch’ where Surber samples were collected. Embeddedness at the ‘patch’ scale (within the quadrat) was estimated using a subjective index (Platts et al. 1983), where 1 was high (>75% fine sediment covering coarse substrate) and 5 low (<5% fine sediment cover).

Sediment depth was recorded at ten points in each reach using a stratified random selection process (Niyogi et al., 2007). A ruler was inserted into soft sediment until underlying,

coarser substratum was reached. Suspendable inorganic sediment (SIS; g/m²) was estimated using the Quorer method (Quinn and Cooper 1997). The benthic substrate in an open drum (30 cm Ø, 0.07 m²) at 15 random locations within the 30 m reach was vigorously disturbed using a steel rod (duration of 30 seconds) to collect 15 replicate samples of suspendable sediment (i.e., a 250 ml water sample taken from the water column inside the open drum). They were processed within 48 hours of collection. To collect the coarsest suspendable sediment, water samples were first filtered through a 125 µm Endecott sieve (Endecotts Ltd, London, UK). The material collected in the sieve was then washed into a pre-weighed aluminum dish and dried, weighed, ashed, and re-weighed. To collect the finer suspendable sediment grains, a sub-sample (50 ml) of the sieved water sample was then filtered through a pre-ashed, pre-weighed filter (LabServ® GF/F, 47 mm Ø), before undergoing the same process. These two estimates of fine inorganic sediment (≥ 125 µm and < 125 µm) were combined (minus the background concentrations of suspended sediment estimated from a 1 L sample of stream water) to give an estimate of total SIS (g/m²).

Finally, a modified ‘Wolman walk’ (Wolman 1954) was used to estimate mean substrate particle size from 100 randomly selected particles. Particles were measured along the longest axis to calculate the mean substrate size. Heterogeneity of particle size was calculated using a sorting index (SI): $SI = 0.5 \times (d_{84}/d_{50} + d_{50}/d_{16})$, where d refers to the stone diameter along the longest axis at the 84th, 50th and 16th fractions respectively (Andrews 1983).

Suspended fine particulate matter (SFPM) was collected using a plankton net (45 µm mesh) suspended in the water column for ten minutes and stored on ice until being frozen in the laboratory. Thawed sub-samples (50 ml) were filtered through a pre-ashed, pre-weighed filter (LabServ® GF/F, 47 mm Ø), dried (48 hours, 50° C), weighed, ashed (6 hours, 550° C), and re-weighed to estimate organic content (resource availability). To estimate periphyton/biofilm

availability (% organic matter and chlorophyll-*a*), five cobbles or sediment samples were collected from random locations. Where fine sediment occurred in large deposits, a glass petri dish (45 mm Ø) was used to remove a circular section of sediment from the stream bed to 7.5 mm deep (Biggs and Kilroy 2000). Individual samples were wrapped in foil, and stored in ice before being frozen. Cobbles or sediment samples were immersed in 100% ethanol for 24 hours (in the dark) at 10° C for pigment extraction. Chlorophyll-*a* was analyzed using the methods for spectrophotometry outlined in Biggs and Kilroy (2000). Filtered sub-samples (LabServ® GF/C, 47 mm Ø) of periphyton (brushed from stones in ethanol) and sediment samples (45 µm Endecott sieve) were dried, weighed, ashed, and re-weighed to estimate % organics. The stones surface area was calculated using the equation of Biggs and Kilroy (2000). Fine and coarse benthic organic matter (g/m² FBOM and CBOM respectively) was estimated from material collected in Surber samples. Material was elutriated, separated using a 2 mm Endecott sieve, dried (48 hours, 50° C), weighed, ashed (4 hours, 550° C), and re-weighed.

Five Surber samples (0.0625 m², 250 µm mesh) were collected from the thalweg of the channel at evenly spaced locations and placed on ice before being frozen. Community data obtained from these samples (Appendix E) were used to calculate qualitative and quantitative response variables at the patch scale (0.0625 m²). An additional composite kick-net sample (250 µm) was collected from each reach to encompass microhabitats (i.e., macrophytes, marginal vegetation, leaf litter) not sampled quantitatively. In the laboratory, samples were passed through a 250 µm Endecott sieve and all invertebrates removed, identified, and counted to the lowest practicable level (usually genus) using invertebrate identification guides (Winterbourn et al. 2006). Taxa presence data from kick-nets were combined with data recorded from the Surber samples to create qualitative response variables (i.e., total and EPT taxa richness) at the reach scale.

Riparian condition was estimated for a 100 m length of stream incorporating the study reach stream using a subjective index of 13 riparian attributes (Harding et al. 2009; Appendix C). Attributes were graded from poor (1) to excellent (5) on each bank, and scores summed to provide an index of riparian habitat quality. For the analysis of total riparian condition and individual attributes, bank scores were averaged to provide a single value for riparian condition at each stream.

Data analysis

Principal components analysis (PCA) in Primer (Version 6.1.12, Primer-E, Lutton, UK) was used to reduce the metrics of deposited fine sediment into a single index (Axis 1 scores; PC1 henceforth, 89% of total variance, Appendix D). Sediment metrics were represented by reach and patch % cover, SIS (g/m^2), and sediment depth (mm). Where appropriate, data were transformed to meet assumptions of analyzes and improve heteroscedasticity (e.g., SIS and dissolved nitrate were log-transformed and % composition data logit-transformed where linear relationships were assumed). Variables were centered (subtracted from sample means) and scaled (divided by sample standard deviation) for analyzes requiring standardized data. To enable model parameterization of PC1, a constant (2) was added to each score to transform negative values to positive figures. Correlation analyzes using Pearson's product-moment and Spearman's rank correlation coefficients (the latter where assumptions of linearity were violated) were used to assess relationships between physico-chemical and biotic variables.

To test the association of deposited sediment, nitrate, and site location (i.e., spatial autocorrelation) with invertebrate community composition, partial redundancy analysis (*pRDA*) was used. We used presence-absence and abundance data to create each biological matrix (Appendix B.2.1). The sediment matrix was composed of four measured components (reach and

patch % cover, SIS, and sediment depth; Appendix E). Nitrate was represented by dissolved nitrate-nitrite nitrogen (mg/L). We represented space (site locations) using a set of spatial variables generated through PCNM analysis (Principal Coordinates of Neighbor Matrices) based on the longitude and latitude of each site (Appendix B.2.2). Residuals that were not explained by sediment, nitrate, or space were considered to be the unexplained variation. Proportions of the total variation attributed to each component were based on the adjusted (unbiased) fractions, which consider in each analysis the total number of predictors and the sample size. The significance of each fraction was tested by permutation tests using 999 randomizations (Peres-Neto et al. 2006). Results of these analyzes were displayed in area-proportional Venn diagrams using ellipses (Appendix B.2.3). Partial RDA analyzes were performed in R using the package “vegan” (Oksanen et al. 2010).

To assess the shape of the relationship between deposited sediment and the relative abundance of sediment-sensitive taxa (% EPT), regression models were selected using an information-theoretic approach (Burnham and Anderson 2002) in conjunction with traditional regression analysis techniques. % EPT is a commonly used index of stream health (Boothroyd and Stark 2000) and refers to the relative abundance of taxa from the insect families Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies). We tested the shape of the relationships of three metrics of deposited fine sediment (patch and reach % cover, SIS) and the sediment index (PC1) with % EPT. The four regression models examined were linear, exponential decay, asymptotic exponential decay, and a 4-parameter sigmoidal curve. These were fitted using the “lm” and “nls” commands in R (R Development Core Team 2010), and the lowest Akaike Information Criterion (AIC_c) values calculated to identify the best-fitting model. Residual statistics (Cook’s Distance) from regression analyzes were then used to identify

potential outliers. Initial regression analyzes indicated that two streams were significant outliers. One of these streams had an intermittent flow regime, and the other was affected by extensive growths of nuisance algae. Thus both streams were omitted from the regression analyzes, and their exclusion did not materially affect the statistical results, although it did improve the fit of the relationships.

To identify sediment thresholds from the relative abundance of sediment-sensitive taxa (% EPT), change-point analysis (CPA) was used. CPA uses a combination of cumulative sum (CUSUM) and bootstrapping techniques (Appendix B.3). Changes in selected invertebrate metrics were detected using Change-Point Analyzer software (Version 2.3, Taylor Enterprises, Libertyville, IL, USA).

Structural equation modeling (SEM) was used to estimate direct and indirect effects between selected physical and biotic variables in causal path models (Grace 2006). Specifically, we used SEM to investigate potential mechanistic pathways influencing invertebrates (% EPT) as mediated by deposited sediment. The sediment index (PC1) was used in both models tested.

We first constructed a SEM (sediment) to investigate the association of sediment with habitat and food availability, and the potential mediated effects of these variables on the relative abundance of sediment-sensitive invertebrates (% EPT). To create an index of habitat availability, substrate embeddedness, mean substrate size (mm), the sorting index (SI), and % of coarse substrate (cobbles and pebbles) were reduced using PCA (Habitat PC1, 78% of total variance, Appendix D). A reach index of chlorophyll-*a* (Appendix B.4) and basal resource quality (% organic matter of periphyton, seston, and fine benthic organic matter) were reduced to create an index of food availability (Food PC1, 55% of total variance, Appendix D).

A second SEM (riparian) was used to investigate the effects of riparian condition (i.e., riparian condition index) mediated through selected physical drivers (dissolved nitrates, flow, and deposited sediment) on % EPT. A pathway between flow (mean stream water velocity, m/s) and sediment was included because it is a strong determinant of sediment accumulation (Lenat et al. 1979).

We chose to report two absolute fit indices, chi-square and the standardized root mean square residual (SRMR), and a relative fit index, the incremental fit index (IFI) for each SEM (Appendix B.5). The two SEMs (sediment and riparian) tested were modeled using the partial least squares approach in PLS Graph (Version 3.0, Soft Modeling Inc, Hosuton, TX, USA); goodness of fit estimates were obtained using the “sem” package in R (Fox, 2010).

RESULTS

Sediment and nutrients

Physico-chemical and biotic parameters for the 30 streams demonstrated variation, particularly for deposited sediment and dissolved nutrients (Table 1). Deposited sediments (cover, depth, and volume) were colinear (Appendix F), and PCA reduced sediment measures into a single index accounting for 89% of total variance (PC1; Appendix D). This combined sediment metric (PC1) was not correlated with dissolved nitrate (Pearson's Product-Moment correlation, $r = 0.14$, $P = 0.48$), dissolved reactive phosphorus (DRP; $r = -0.23$, $P = 0.23$), water temperature ($r = 0.10$, $P = 0.58$), or dissolved oxygen ($r = -0.15$, $P = 0.43$). Nitrate and DRP were also not correlated ($r = -0.03$, $P = 0.89$). The concentration of DRP was relatively low in the vast majority of streams sampled, and is unlikely to be a major driver of enrichment in these streams (Greenwood et al. 2012).

TABLE 1. Abiotic and biotic characteristics of 30 streams surveyed across the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Two different spatial scales were assessed; reach (30 m) and patch (0.0625 m²). Patch samples ($n = 5$) were located within the study reach. DRP: dissolved reactive phosphorus; SIS: suspendable inorganic sediment; EPT: Ephemeroptera, Plecoptera, Trichoptera (sediment-sensitive insect orders).

Spatial scale	Method and replication	Variable	Median	Min	Max
Chemical variables					
Reach	Filtered water sample (SYSTEAs Easychem discrete colorimetric auto-analyzer)	NO ₃ -N (mg/L)	2.3	0.03	8.8
		DRP (µg/L)	11	3	126
	Direct measurement (YSI 63 meter)	Conductivity (µS _{25° C} /cm)	142	64	323
		pH	7.4	6.8	8.0
	Direct measurement (YSI 550A meter)	Temperature (°C)	13.9	11.5	17.3
		Dissolved oxygen (%)	91	57	118
Physical variables					
Patch	Visual assessment (5 quadrats, 0.0625 m ²)	Substrate embeddedness	2.7	0.8	5.0
		% Sediment cover (patch)	14	0	100
Reach	Visual assessment (10 quadrats, 0.09 m ²)	% Sediment cover (reach)	20	1	100
	Direct measurement (10 depths)	Sediment depth (mm)	9	0.3	364
	15 ‘Quorer’ samples (Quinn and Cooper 1997)	SIS (g/m ²)	284	11	17,800
	Direct measurement (100 stones)	Mean substrate size (mm)	26.3	1.3	72.4
	3 stream transects	Mean discharge (m ³ /s)	0.11	0.01	0.45
		Mean stream width (m)	3.1	1.5	5.9
	3 stream transects (10 measurements per transect)	Mean water depth (m)	0.16	0.09	0.39
		Mean flow (m/s)	0.18	0.02	0.53
	Subjective index (Harding et al. 2009)	Riparian condition	42.0	28.5	55
	Biological variables				
Patch	Surber sample (5 reps, 0.0625 m ²)	Density (no. ind./0.0625 m ²)	1,080	436	3,461
		Mean taxa richness	27	19	42
		Mean EPT richness	8	3	14
		% EPT (relative abundance)	27	1	94
Reach	5 stone and/or sediment samples	Chlorophyll- <i>a</i> (mg/m ²)	15	4	228
	5 Surber (0.0625 m ²) and 1 composite kick-net sample	Taxa richness	53	40	64
		EPT richness	16	7	23

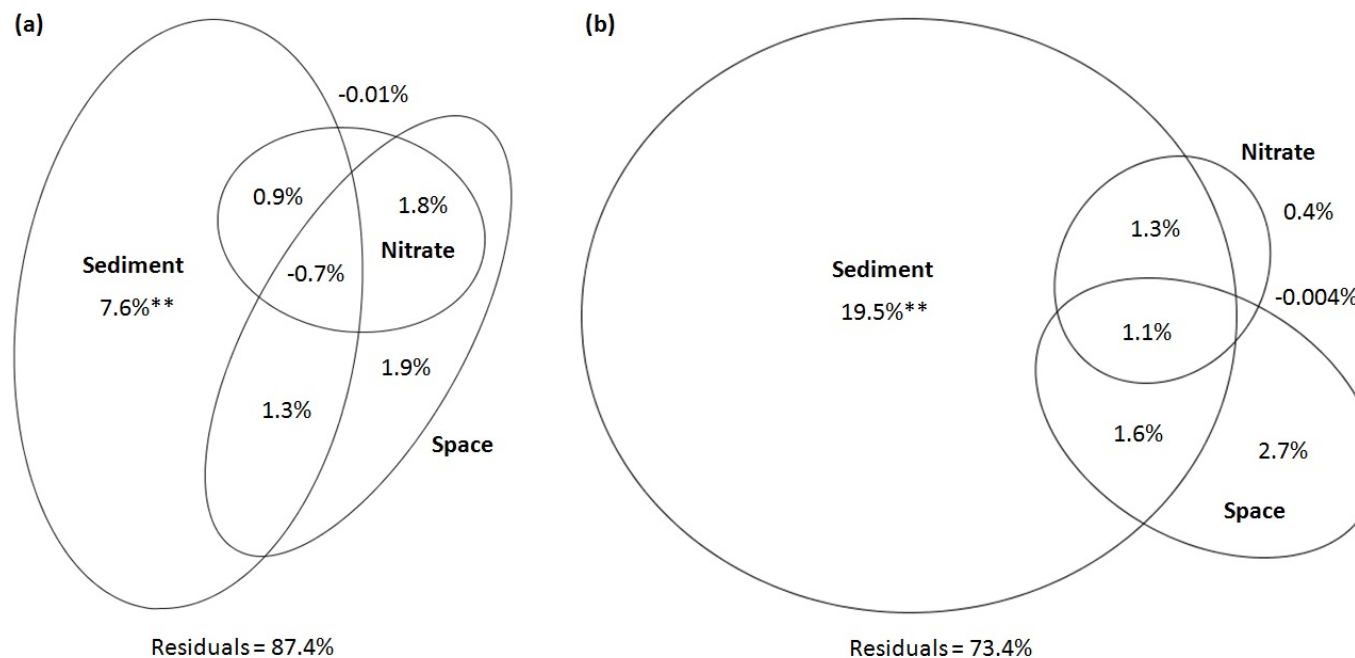


FIG. 1. Results of variation partitioning in the partial redundancy analysis (*pRDA*) of stream invertebrate communities surveyed across the Canterbury Plains, South Island, New Zealand during the austral summer of 2009–2010. (a) Presence-absence and (b) abundance data to compose the biological matrix, four measures of sediment (patch and reach % sediment cover, SIS, and depth) to compose the sediment matrix, dissolved nitrate-nitrite nitrogen data to represent nitrate (nutrients), and the spatial matrix (space) of six variables was composed from study site longitude and latitude data using Principal Coordinates of Neighbors Matrices analysis (PCNM). Area-proportional Venn diagrams using ellipses show the pure effects of sediment, nitrate and space on community composition, with the intersections representing the covariation between these predictors. The explained variation of these predictors is based on the adjusted R^2 , and the residuals represent unexplained variation. ** $P < 0.01$.

*p*RDA of invertebrate community data attributed 7.6% of total variance in the presence-absence of invertebrate taxa to deposited sediment (Fig. 1a); a permutation test indicated that this was significant ($P < 0.01$). The second *p*RDA attributed 19.5% of total variance in the abundance of invertebrates to deposited sediment (Fig. 1b), a contribution that was significant ($P < 0.01$). No other variables (space or nitrate), or their covariance with sediment, significantly explained variance in invertebrate community composition in either *p*RDAs.

Inspection of the taxa-specific responses indicated that abundance of EPT taxa, including the mayfly *Deleatidium* (Leptophlebiidae) and the caddisflies *Pycnocentrodes* and *Pycnocentria* (Conoesucidae) were most strongly negatively correlated with *p*RDA axis 1, whereas taxa positively correlated with this axis included ostracods, nematode worms, and the snail *Potamopyrgus antipodarum* (Appendix E). This reflected the strong correlation of deposited sediment variables with *p*RDA axis 1.

Univariate responses to sediment

The relative proportion of EPT showed a strong sigmoidal response to sediment (Fig. 2). Using AIC_c values, a 4-parameter sigmoidal curve was the best fitting model (Appendix G) for the relationship between sediment (PC1) and % EPT (Fig. 2a), with CPA identifying a threshold at -0.31 (Appendix H). Similarly, the same sigmoidal model was the best fit (Appendix G) for the response of % EPT to % sediment cover at the reach scale (Fig. 2b) and for suspendable inorganic sediment (SIS, g/m^2 ; Fig. 2c). CPA demonstrated that at the reach scale, a change occurred at approximately 20% sediment cover (95% confidence interval, 18-21%), or at 155 g/m^2 SIS (63-244 g/m^2 ; Appendix H). The relationship between sediment and % EPT at the patch scale (Fig. 2d) was best fit with an asymptotic exponential decay curve (Appendix G), and CPA indicated that a threshold of change at this spatial scale occurred at approximately 13% sediment cover (Appendix H). This lower threshold reflects

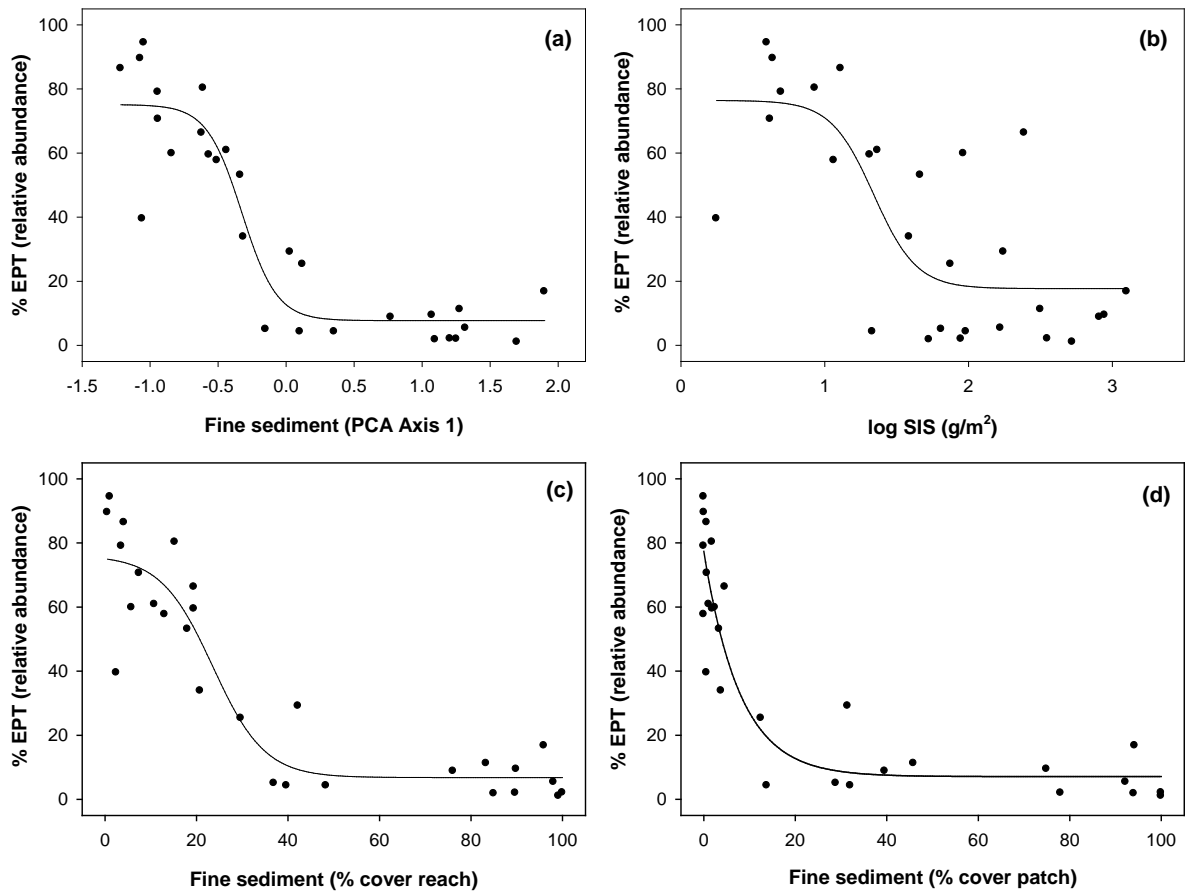


FIG. 2. (a) Relationship between Sediment (PC1) and % EPT fitted as a four-parameter sigmoidal curve $y = a + b/(1 + e^{-(x-c)/d})$ with parameter estimates $a = 7.7 \pm 3.7$ (mean \pm 1 SE; $P < 0.05$), $b = 67.3 \pm 6.5$ ($P < 0.001$), $c = 1.67 \pm 0.06$ ($P < 0.001$), and $d = -0.13 \pm 0.05$ ($P < 0.05$); (b) Relationship between suspendable inorganic sediment (SIS; g/m²) and % EPT fitted as a four-parameter sigmoidal curve $y = a + b/(1 + e^{-(x-c)/d})$ with parameter estimates $a = 17.7 \pm 6.6$ ($P < 0.05$), $b = 58.7 \pm 13.2$ ($P < 0.001$), $c = 3.09 \pm 0.32$ ($P < 0.001$), and $d = -0.34 \pm 0.31$ ($P = 0.28$); (c) Relationship between % sediment cover (reach) and % EPT fitted as a four-parameter sigmoidal curve $y = a + b/(1 + e^{-(x-c)/d})$ with $a = 6.8 \pm 3.9$ ($P = 0.096$), $b = 69.3 \pm 8.4$ ($P < 0.001$), $c = 23.5 \pm 2.7$ ($P < 0.001$), and $d = -5.7 \pm 2.5$ ($P < 0.05$); (d) Relationship between % sediment cover (patch) and % EPT fitted as a three-parameter exponential curve, $y = a + be^{-cx}$ with $a = 7.1 \pm 3.9$ ($P = 0.08$), $b = 70.1 \pm 5.9$ ($P < 0.001$), $c = -0.13 \pm 0.04$ ($P < 0.01$).

the generally lower levels of deposited sediment in the channel thalweg. Overall, our results indicate a strong threshold effect of deposited sediment, as the invertebrate community shifts from a community dominated by mayflies and caddisflies to one characterised by non-insect invertebrates including micro-crustaceans, molluscs, and worms.

Pathways of potential sediment effects

The sediment SEM revealed that deposited sediment negatively affected both food and habitat availability. However, this association with % EPT was only significantly mediated through the modification and loss of benthic habitat (i.e., habitat availability; Fig. 3a). The goodness of fit measures we used suggested the sediment model was appropriate, with the chi-square test ($\chi^2 = 2.08$, $P = 0.15$), SRMR (< 0.05) and the IFI (> 0.99) all indicating an adequate model fit.

The riparian SEM indicated that ‘poor’ riparian condition contributed to increased levels of deposited sediment. Riparian condition had an indirect effect on sediment mediated through flow, with ‘good’ riparian condition being associated with higher flow velocities leading to lower levels of deposited sediment. However, it had no significant association with nitrate concentrations (Fig. 3b). In turn, there was a significant effect of sediment on % EPT (Fig. 3b). The chi-square test model ($\chi^2 = 0.838$, $P = 0.840$), SRMR (< 0.05) and the IFI (> 0.99) all indicated adequate model fit for the riparian SEM.

DISCUSSION

Our results show that marked declines in pollution-sensitive taxa (% EPT) leading to changes in community composition were strongly associated with deposited fine inorganic sediment (< 2 mm), and that the non-linear response of % EPT combined with change-point analysis suggested a threshold of approximately 20% sediment covering the streambed at the reach scale. This threshold value has been robustly elucidated, and is important to help better

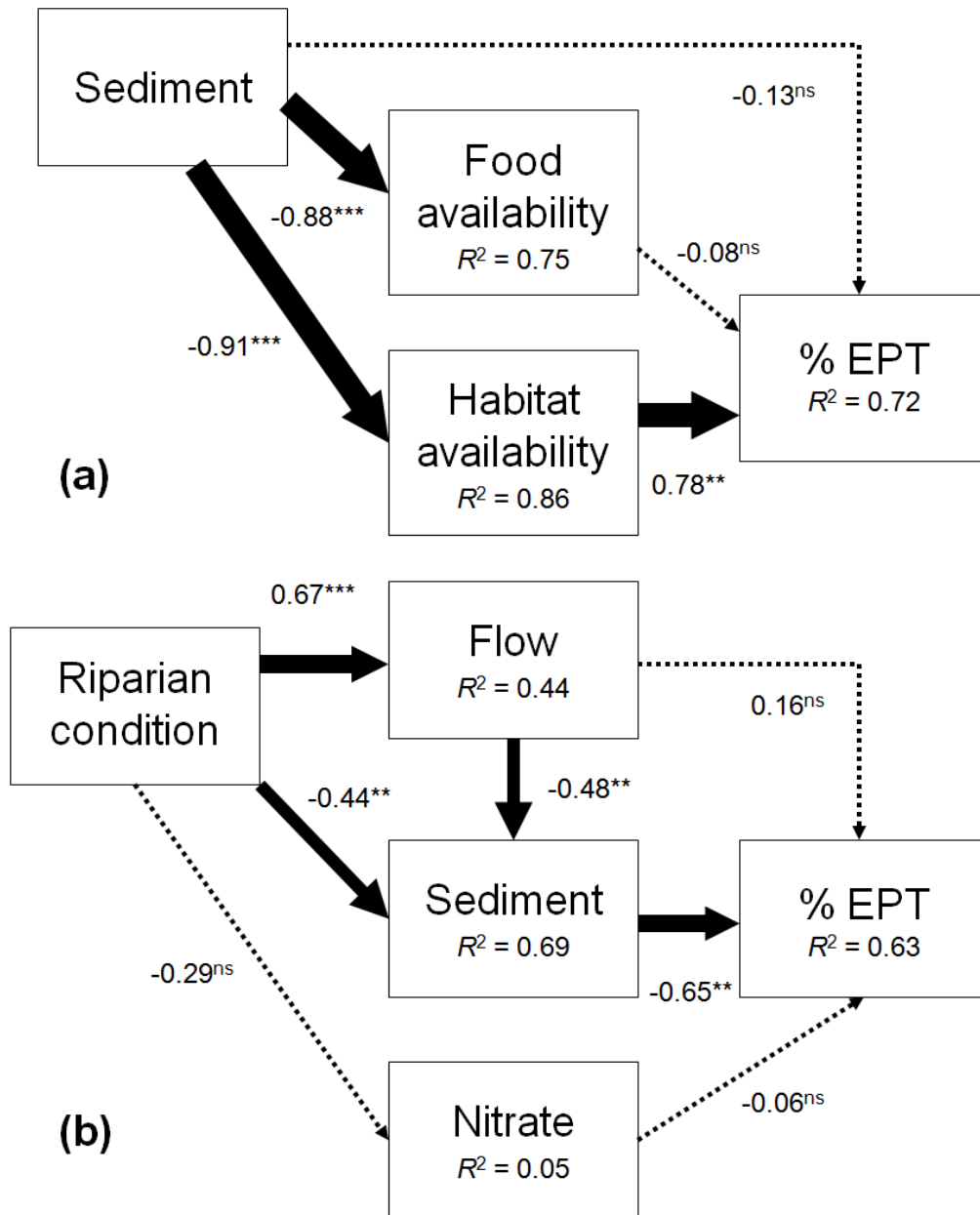


FIG. 3. (a) Sediment and (b) riparian structural equation models (SEM) show potential causal pathways affecting % EPT. Non-significant paths are indicated by dotted arrows. The thickness of the solid arrows reflects the magnitude of the standardized SEM coefficients. Bootstrapped standardized coefficients are listed beside each path, and significance levels based on a two-tailed t-statistic calculated from coefficient means. For the endogenous variables used in the two models, squared multiple correlations (R^2) indicate the variance explained by all associated pathways linking that variable. ** $P < 0.01$, *** $P < 0.001$.

guide management efforts to protect and rehabilitate streams in modified catchments. This threshold appeared to be strongly driven by the loss of benthic habitat through the infilling of interstitial spaces and the burial of coarse substrate. Evidence of a lower threshold (13%) at the patch-scale reflected the generally lower levels of deposited sediment relative to the stream reach in the channel thalweg where quantitative invertebrate samples were collected. However, the 95% confidence interval for this threshold suggests that as little as 4% sediment cover could have an adverse effect on benthic invertebrate communities. These lower levels have the potential to be more useful for ‘pristine’ streams where deposited sediment levels have been historically low or where sediment fluxes are dynamic. The strong effect of sediment on the relative abundance of EPT corroborates the findings of other studies conducted in New Zealand (Townsend et al. 2008), Wales (Larsen et al. 2009), and West Virginia, USA (Angradi 1999). These studies found that sediment can have a strong effect upon EPT taxa richness and abundance, although none identified a threshold response to this stressor.

Deposited sediment thresholds

Few published studies have demonstrated strong evidence of meaningful sediment thresholds from either field survey data or experimental manipulations, despite a plethora of different sediment criteria and standards being used in countries such the USA (Benoy et al. 2012) and New Zealand (Clapcott et al. 2011). In one of the few exceptions, Kaller and Hartman (2004) presented evidence that EPT taxa richness significantly decreased in streams where very fine inorganic sediment particles (<0.25 mm) exceeded 0.8–0.9% of riffle substrate composition. Jessup et al. (2010) provided evidence that corroborates our estimated threshold value of 20% at the reach scale. They used a combination of LOESS regression and change-point analysis to identify a surficial sediment threshold of <20% fines for sediment-sensitive stream invertebrates in 136 mountain streams sampled across the southwestern USA.

However, Bryce et al. (2010) calculated threshold values of 13% to protect sediment-sensitive aquatic vertebrates and 10% for macroinvertebrates in 557 mountain streams of the western USA; figures closer to our estimated value of 13% at the patch scale. More recently, Benoy et al. (2012) attempted to establish sediment thresholds for stream invertebrates in New Brunswick, Canada using regression trees and change-point analyzes. In the 15 agricultural streams they surveyed, the ecological threshold (14.8%) for the relative abundance of EPT taxa in response to surface fines (<2 mm) fell between our estimated values at the patch and reach scale.

Our approach to record multiple measurements of sediment at different scales indicates that sampling resolution and methods can have an impact upon observed results. The discrepancy in our estimated thresholds at the patch and reach scales was expected, given that we quantitatively sampled the thalweg of the channel across all streams for invertebrate densities. By consistently sampling the deepest and fastest flowing part of the channel, we avoided natural areas of deposition at the margins of the channel and those in macrophyte beds. Thus, although patch-scale sediment cover was the more accurate scale to measure for invertebrate responses, a sediment threshold at the reach scale is more realistic for stream monitoring. In contrast, Larsen et al. (2009) found that reach-scale sediment levels correlated poorly with patch-scale invertebrate data. This may have been exacerbated by the relatively low levels of deposited sediment in their streams (i.e., maximum sediment cover ~ 30%). Nevertheless, their study and our results further demonstrate the importance of considering spatial scale when looking for critical thresholds, either theoretically or empirically (Homan et al. 2004).

Mechanisms driving sediment thresholds

Although the elucidation of sediment thresholds is extremely important for effective management, they do not reveal the mechanisms driving changes in invertebrate communities.

The reduction of resource availability (habitat and food) by sedimentation could exert strong effects on EPT fauna at different life-history stages (e.g., egg, larvae, and pupae). In our study, habitat availability (i.e., interstitial spaces and associated coarse substrate) was more important than food availability and any unmeasured direct effects of sediment (e.g., adsorbed toxicants) in explaining the relative abundance of EPT. The combined effects of habitat loss could help explain the non-linear relationship of % EPT with deposited sediment, and reflect the degree of infilling of interstices. Benoy et al. (2012) were able to associate their surficial sediment threshold with the proportion of interstitial fines, and Ryder (1989) found that a 12-17% increase in interstitial sediment resulted in a 27-55% decrease in the abundance of the mayfly *Deleatidium*. In contrast, colonization trials showed that the occurrence of fine sediment in the algal matrix reduced mayfly densities by nearly 30%, suggesting that habitat loss may be more important than decreased food quality to sediment-sensitive stream invertebrates.

Models based on percolation theory suggest that as the percentage of habitat loss increases, patch size decreases and isolation increases in a non-linear fashion (Homan et al. 2004). Consequently the relationship between habitat loss and species populations may also be non-linear, and crossing these thresholds may lead to alternative stability domains, or stable states characterized by altered community composition (Scheffer et al. 1993).

‘Alternative stable states’ refer to phenomena that involve both threshold and hysteretic behavior (i.e., a system moves to a new ‘domain of attraction’, and cannot easily return). We suggest this framework is appropriate, given the loss of habitat exerted by sediment where inputs exceed the ‘assimilative capacity’ of a stream (Waters 1995). Hysteretic behavior implies that deposited sediment may require greater reduction below established impact thresholds for effective stream rehabilitation. Moreover, it is unknown how much increased substrate instability might contribute to a threshold effect of habitat loss, although Australian

research suggests that the infilling of interstitial spaces may be more important than interactive effects of hydrodynamic disturbance (Bond and Downes 2003). Although many of the identified effects of fine sediment on macroinvertebrates occur as a consequence of deposition, most current management guidelines for sediment management are based on suspended sediment targets and thus are unlikely to be appropriate for the purpose of effective management (Jones et al. 2011). Results of previous studies, combined with our findings, demonstrate that impact thresholds to deposited sediment may be particularly relevant for the protection and rehabilitation of streams in modified catchments, and thus need to be well understood by scientists and managers to better guide management efforts.

Potential impacts of sediment and nutrients

Our study has demonstrated clear thresholds in deposited sediment that have significant associations with invertebrate community composition. Sediment removes and homogenizes habitat (Waters 1995), and changes to community composition suggest a strongly deterministic response reflecting niche processes. Substrate heterogeneity, which has a strong positive correlation with diversity in running waters (Poff and Ward 1990) is often attributed to a "greater number of niches" in more heterogeneous habitat (Beisel et al. 2000). However, the complete extirpation of highly mobile stream invertebrates in response to physical disturbance may be uncommon, reflecting rapid recolonization following a perturbation (McCabe and Gotelli 2000). The effect of physical disturbance on stream invertebrate diversity may also be influenced by interactions with other factors including habitat heterogeneity (e.g., patchiness) and productivity (Death and Winterbourn 1995). In our study, although changes to invertebrate community composition (taxa presence and absence) indicated some species turnover; overall taxa richness did not change significantly along the sediment gradient (F. J. Burdon, *unpublished data*). Temporal variation in perturbations may have influenced diversity patterns (Molinos and Donohue 2011). Additionally, these patterns

may also have reflected the overall degraded nature of the study area by agricultural land uses and the reduced regional species pool, with sensitive taxa such as stoneflies (Plecoptera) largely absent from these lowland streams. However, despite the agricultural context of our study, the strong response to sediment by EPT taxa including the leptophlebiid mayfly *Deleatidium* and the conoesucid caddisflies *Pycnocentroides* and *Pycnocentria*, three common and widespread stream insects found in New Zealand (Winterbourn et al. 1981), suggests a widely applicable result. This is important, because such changes associated with deposited sediment may cascade up to higher consumers (Osmundson et al. 2002). For example, reduced abundances of EPT could propagate across stream boundaries, affecting riparian consumers that use adult aquatic insects as a prey subsidy (Burdon and Harding 2008).

In contrast, although dissolved nitrate did not explain community composition well, this stressor was negatively correlated with taxa richness (F. J. Burdon, *unpublished data*), thus confirming trends observed in other studies elsewhere (Yuan 2010). Nitrate can have an impact on invertebrates through direct toxicity (Camargo and Alonso 2006) and indirectly through increased primary production reducing dissolved oxygen (Dodds and Welch 2000) or smothering benthic habitat with filamentous algae (Ortiz and Puig 2007). Recent studies involving nutrient enrichment of streams and basal resources have demonstrated shifts in benthic macroinvertebrate communities toward lower diversity (Gafner and Robinson 2007) and nutrient-induced changes to resource quality may facilitate competitive exclusion (Evans-White et al. 2008). In our study, the weak association of nitrate with community composition may reflect the varying concentrations present in upwelling groundwater decoupling this stressor with other drivers of change in agricultural streams (e.g., degraded riparian condition, altered flows, and sedimentation). These potential effects warrant further investigation and reinforce the need for managers to consider the effects of multiple stressors in modified catchments (Townsend et al. 2008).

Riparian condition and flow regimes

The loss of riparian vegetation (Allan 2004) and inputs of sediment associated with agriculture are well documented (Walling 1990). Our results suggest that degraded riparian condition may contribute directly and indirectly to sediment dynamics in streams. The direct effects appeared to be the consequence of current land use practices involving excessive livestock access to the riparian zone and runoff from rills and channels (F. J. Burdon, *unpublished data*); however, the lack of significant associations with other variables including riparian understory and type suggest ongoing legacy effects from past land management practices (Harding et al. 1998). Despite this, our results indicate that management strategies reducing sediment inputs including riparian fencing to exclude livestock may be useful for protecting and enhancing instream habitat. Unmanaged grazing is well recognized as having deleterious effects upon riparian and instream habitat through bank erosion and channel over-widening, and these effects can lead to altered invertebrate community composition and loss of pollution-sensitive taxa (Herbst et al. 2012). In our study, high-intensity riparian grazing appeared to have a negative effect on stream communities through increased inputs of sediment, with an indirect effect mediated through reduced flow velocities (thus aiding sediment deposition) that appeared to only partly be explained by channel over-widening. Other factors that may have contributed to sediment deposition include channel straightening and maintenance, which can lead to more diffuse and homogenous distribution of fine substrate (Harrison et al. 2004), and excessive growth of invasive macrophytes, which can retain large quantities of deposited sediment (Bunn et al. 1998).

More sluggish stream flows may also have been a reflection of localized land use intensity, including groundwater extraction for irrigation. Streams that experience low flows as a result of water abstraction for irrigation and drought can also have increased levels of fine sediment deposition (Wood and Petts 1994). Carlisle et al. (2010) showed that across multiple

regions of the USA, the likelihood of stream biological impairment doubled with increasing severity of diminished flows. Experimental work by Matthaei et al. (2010) corroborated these findings by demonstrating that flow reduction and fine sediment additions interact to cause significantly more harm. This is because lower flows reduce the ability of streams and rivers to mobilize and remove deposited sediment, highlighting the connection between flow regime and instream habitat. Indeed, flow can be considered a ‘master variable’ that limits the distribution and abundance of biota and regulates the ecological integrity of stream ecosystems (Poff et al. 1997). Our results demonstrated that flow had a strong indirect effect on sediment-sensitive invertebrates mediated through sediment deposition.

Concluding remarks

Our results demonstrate a strong influence of sediment on pollution-sensitive taxa (% EPT), and our threshold effects of 13-20% surficial sediment corroborates similar figures reported in North America. Although the validation of this threshold with experimental manipulations will be essential, this figure has been robustly derived and should encourage managers to develop consistent sediment criteria and standards within regions. Managers need to be aware that human actions can result in rapid changes leading to potentially undesirable alternative stable states, with recovery demanding far more resources and time than those required by prevention (Dodds et al. 2010). As a final comment, the strong nexus between sediment dynamics and stream flow regimes suggests a growing threat from the intensification of agriculture, population growth, and potentially, climate change (IPCC 2001). Addressing such problems will require collaboration of experts across multiple disciplines.

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LITERATURE CITED

- Allan, D. J. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257-284.
- Allan, D. J., D. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37:149-161.
- American Public Health Association (APHA). 1995. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC, USA.
- Angradi, T. R. 1999. Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society* 18:49-66.
- Andrews, E. D. 1983. Entrainment of gravel from naturally sorted riverbed material. *Geological Society of America Bulletin*. 94:1225-1231.
- Armour, C. L., D. A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. *Fisheries* 16:7-11.
- Baldy, V., V. Gobert, F. Guerold, E. Chauvet, D. Lambrigot, and J. Y. Charcosset. 2007. Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved

- inorganic nutrients on microorganisms and invertebrates. *Freshwater Biology* 52:1322-1335.
- Beisel, J. N., P. Usseglio-Polatera, and J. C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422:163-171.
- Benoy, G. A., A. B. Sutherland, J. M. Culp, and R. B. Brua. 2012. Physical and ecological thresholds for deposited sediments in streams in agricultural landscapes. *Journal of Environmental Quality* 41:31-40.
- Berkman, H., and C. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285-294.
- Biggs, B. J. F., and C. Kilroy. 2000. *Stream Periphyton Monitoring Manual*. Ministry for the Environment, Wellington, New Zealand.
- Bond, N. R., and B. J. Downes. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* 48:455-465.
- Boothroyd, I., and J. D. Stark. 2000. Use of invertebrates in monitoring. Pages 344-373 in K. J. Collier and M. J. Winterbourn, editors. *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society, Christchurch. New Zealand.
- Braccia, A., and J. R. Voshell. 2007. Benthic macroinvertebrate responses to increasing levels of cattle grazing in Blue Ridge Mountain streams, Virginia, USA. *Environmental Monitoring and Assessment* 131:185-200.
- Bryce, S. A., G. A. Lomnický, and P. R. Kaufmann. 2010. Protecting sediment sensitive aquatic species in mountain streams through the application of biologically based criteria

- streambed sediment criteria. *Journal of the North American Benthological Society* 29:657–672.
- Bunn, S. E., P. M. Davies, D. M. Kellaway, and I. P. Prosser. 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* 39:171-178.
- Burdon, F. J., and J. S. Harding. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology* 53:330-346.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Camargo, J. A., and Á. Alonso. 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. *Environment International* 32:831-849.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264–270.
- Clapcott, J. E., R. G. Young, J. S. Harding, C. D. Matthaei, J. M. Quinn, and R. G. Death. 2011. Sediment assessment methods: protocols and guidelines for assessing the effects of deposited fine sediment on in-stream values. Cawthron Institute, Nelson, New Zealand.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76:1446-1460.
- Dodds, W. K., W. H. Clements, K. Gido, R. H. Hilderbrand, and R. S. King. 2010. Thresholds, breakpoints, and nonlinearity in freshwaters as related to management. *Journal of the North American Benthological Society* 29:988-997.

- Dodds, W. K., and E. B. Welch. 2000. Establishing nutrient criteria in streams. *Journal of the North American Benthological Society* 19:186-196.
- Evans-White, M. A., W. K. Dodds, D. G. Huggins, and D. S. Baker. 2008. Thresholds in macroinvertebrate biodiversity and stoichiometry across water-quality gradients in Central Plains (USA) streams. *Journal of the North American Benthological Society* 28:855-868.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629-644.
- Fox, J., with contributions from A. Kramer and M. Friendly. 2010. *sem: Structural equation models*. R package. R Foundation for Statistical Computing, Vienna, Austria.
- Gafner, K., and C. T. Robinson. 2007. Nutrient enrichment influences the response of stream macroinvertebrates to disturbance. *Journal of the North American Benthological Society* 26:92-102.
- Grace, J. B. 2006. *Structural equation modeling and natural systems*. Cambridge University Press Cambridge, UK.
- Greenwood, M. J., J. S. Harding, D. K. Niyogi, and A. R. McIntosh. 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology* 49:213-222.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95:14843-14847.
- Harding, J. S., R. G. Young, J. W. Hayes, K. A. Shearer, and J. D. Stark. 1999. Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology* 42:345-357.
- Harding, J. S., J. Clapcott, J. Quinn, J. Hayes, M. Joy, R. Storey, H. Greig, J. Hay, T. James, M. Beech, R. Ozane, A. Meredith, and I. Boothroyd. 2009. Stream habitat assessment

- protocols for wadeable rivers and streams of New Zealand. School of Biological Sciences, University of Canterbury Christchurch, New Zealand.
- Harrison, S. S. C., J. L. Pretty, D. Shepherd, A. G. Hildrew, C. Smith, and R. D. Hey. 2004. The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology* 41:1140-1154.
- Haynes, R. J., and G. S. Francis. 1990. Effects of mixed cropping farming systems on changes in soil properties on the Canterbury Plains. *New Zealand Journal of Ecology* 14:73-82.
- Herbst, D. B., M. T. Bogan, S. K. Roll, and H. D. Safford. 2012. Effects of livestock exclusion on in-stream habitat and benthic invertebrate assemblages in montane streams. *Freshwater Biology* 57:204-217.
- Homan, R. N., B. S. Windmiller, and J. M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14:1547-1553.
- IPCC. 2001. *Climate change 2001: The scientific basis*. Cambridge University Press, Cambridge, UK.
- Jessup, B. K., D. Eib, L. Guevara, J. Hogan, F. John, S. Joseph, P. Kaufmann, and A. Kosfisz. 2010. *Sediment in New Mexico streams: existing conditions and potential benchmarks*. Prepared for the U.S. Environmental Protection Agency, Region 6, Dallas, TX and the New Mexico Environment Department, Santa Fe, NM. Prepared by Tetra Tech, Inc., Montpelier, VT, USA.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2011. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055–1071.

- Kaller, M. D., and K. J. Hartman. 2004. Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia* 518:95-104.
- Larsen, S., I. P. Vaughan, and S. J. Ormerod. 2009. Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biology* 54:203-219.
- Lenat, D. R., D. L. Penrose, and K. W. Eagleson. 1979. Biological evaluation of non-point source pollutants in North Carolina streams and rivers. North Carolina Department of Natural Resources and Community Development, Biological Series 102. Raleigh, NC, USA.
- MacLeod, C. J., and H. Moller. 2006. Intensification and diversification of New Zealand agriculture since 1960: an evaluation of current indicators of land use change. *Agriculture, Ecosystems and Environment* 115: 201-218.
- Maloney, K. O., and D. E. Weller. 2010. Anthropogenic disturbance and streams: land use and land-use change affect stream ecosystems via multiple pathways. *Freshwater Biology* 56:611–626.
- Matthaei, C. D., J. J. Piggott, and C. R. Townsend. 2010. Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology* 47:639-649.
- McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124:270-279.
- Molinos, J. G., and I. Donohue. 2011. Temporal variability within disturbance events regulates their effects on natural communities. *Oecologia* 166:795-806.
- Niyogi, D., M. Koren, C. Arbuckle, and C. Townsend. 2007. Stream communities along a catchment land-use gradient: subsidy-stress responses to pastoral development. *Environmental Management* 39:213-225.

- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner 2010. *Vegan: community ecology package*. R Foundation for Statistical Computing, Vienna, Austria.
- Osmundson, D. B., R. J. Ryel, V. L. Lamarra, and J. Pitlick. 2002. Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. *Ecological Applications* 12:1719-1739.
- Ortiz, J. D., and M. A. Puig. 2007. Point source effects on density, biomass and diversity of benthic macroinvertebrates in a Mediterranean stream. *River Research and Applications* 23:155-170.
- Pangborn, M. C., and K. B. Woodford. 2011. Canterbury dairying - a study in land use change and increasing production. Proceedings of the 18th International Farm Management Congress, Methven, Canterbury, New Zealand. International Farm Management Association, Cambridge, UK.
- Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614-2625.
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. General Technical Report INT-138. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769-784.
- Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.

- Quinn, J. M., and A. B. Cooper. 1997. Land–water interactions at Whatawhata, New Zealand: introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research* 31:569–577.
- R Development Core Team, 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ryder, G. I. 1989. Experimental studies on the effects of fine sediments on lotic invertebrates. Ph.D thesis. University of Otago, Dunedin, New Zealand.
- Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8:275-279.
- Sponseller, R. A., E. F. Benfield, and H. M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409-1424.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.
- Townsend, C. R., S. S. Uhlmann, and C. D. Matthaei. 2008. Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology* 45:1810-1819.
- Tylianakis, J. M., T. Tcharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202-205.
- USEPA (US Environmental Protection Agency). 2000. The quality of our nation's waters: a summary of the National Water Quality Inventory. 1998 report to Congress. EPA-841-S-001. Office of Water, US Environment Protection Agency, Washington DC, USA.

- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Walling, D. E. 1990. Linking the field to the river: sediment delivery from agricultural land. Pages 129-152 in J. Boardman, D. L. Foster and J. A. Dearing, editors. *Soil erosion on agricultural land*. Wiley, Chichester, UK.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.
- Waters, T. F. 1995. *Sediment in streams: sources, biological effects, and control*. American Fisheries Society Monograph 7. Bethesda, Maryland, USA.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* 30:377-392.
- Winterbourn, M. J., K. L. D. Gregson, and C. H. Dolphin. 2006. Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand* 14.
- Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15:321-328.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35:951-956.
- Wood, P. J., and G. E. Petts. 1994. Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management* 9:303-316.
- Yuan, L. L. 2010. Estimating the effects of excess nutrients on stream invertebrates from observational data. *Ecological Applications* 20:110-125.

SUPPLEMENTAL MATERIAL

Appendix A

Map and table describing site locations and basic physico-chemical parameters.

Appendix B

Detailed descriptions of specific variables and statistical methods used in analyzes.

Appendix C

Variables used to calculate a subjective index of riparian condition.

Appendix D

Results from principal component analyzes used to reduce variables.

Appendix E

Invertebrate community abundance data and results of partial redundancy analysis.

Appendix F

Relationships of measured variables used for deposited sediment index.

Appendix G

AIC_c values used to select univariate regression models.

Appendix H

Results of change-point analyzes identifying sediment thresholds.

CHAPTER 3: PREAMBLE

Chapter 3 considers the second question posed in my literature review (Chapter 1): Do changes to communities affect food-web properties? In Chapter 2, sediment exerted a strong influence on invertebrate community structure, reflecting a non-linear response by %EPT (Ephemeroptera, Plecoptera, Trichoptera) to deposited sediment. However, less clear was the functional consequences of this change, and whether species turnover was sufficient to maintain trophic structure (Leibold et al. 1997). Moreover, although previous studies have considered the effects of sediment on community structure and function, this has often been done using invertebrate or fish data alone using traditional indices (e.g., functional-feeding groups). Few studies have attempted to characterize entire stream food webs along a sediment gradient. This study links in with many of the postulates discussed in the review chapter (Chapter 1), and focuses on three key predictions: sedimentation affects (1) food-chain length (i.e., vertical structure), (2) effective resource breadth (i.e., horizontal structure), and consequently, (3) community trophic niches in stream ecosystems. To evaluate these predictions, I surveyed stream communities and food webs along a sedimentation gradient, in a subset of 12 streams from the larger survey documented in Chapter 2.

LITERATURE CITED

Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467-494.

CHAPTER 3

NICHE-SPACE COMPRESSION INFLUENCED BY SEDIMENTATION IN AGRICULTURAL STREAM FOOD WEBS



A relatively sediment-free stream near the Waimakariri River, Canterbury Plains.

Abstract. Agriculture dominates human land uses spatially, and is intensifying to meet the demands of world population growth. This is contributing to widespread ecosystem change by altering species distributions and pervasively affecting biotic interactions. Sedimentation is a major pathway by which agriculture exerts pressure on stream ecosystems. Although effects of fine inorganic sediment on aquatic biota are well recognized, how these changes influence the properties of stream food webs is less well understood. We investigated effects of sedimentation on stream food webs by analysing invertebrate and fish community composition and stable isotopes from twelve agricultural streams along a deposited sediment gradient. Taxa richness in both communities declined markedly with increasing sediment deposition. Sediment influenced invertebrate community composition, reflecting a strong decline in the relative abundance of sediment-sensitive insects; however, it had no significant effect on fish assemblages. Structural food-web properties based on stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) obtained from invertebrates and fish indicated sediment reduced trophic diversity. The reduction in trophic area reflected a narrowing of the consumer $\delta^{13}\text{C}$ range, thus suggesting that sedimentation reduced the effective resource niche breadth of stream communities. However, there was no significant association of food-chain length with sediment. Potential mechanisms causing a reduction in trophic diversity include the loss of specialist invertebrates and a greater reliance by primary consumers on detritus (e.g., fine particulate organic matter). The effects of sediment disturbance on food-web structure may alter interactions, thus causing decreased ecosystem function and stability. Our results go further than traditional indices in describing functional changes to stream ecosystems, and indicates that habitat degradation and reduced resource heterogeneity associated with sedimentation contributes to a ‘compression’ of trophic niche space.

Keywords: disturbance; fine inorganic sediment; food-chain length; global change; niche space; stable isotopes; stream communities; trophic niche

INTRODUCTION

The world's ecosystems are facing unprecedented rates of change, driven in part by extensive habitat loss and degradation associated with intensive human land uses (Tylianakis et al. 2008). Agricultural land uses dominate much of the earth's terrestrial ecosystems and are likely to continue intensifying to meet the demands of world population growth (Vitousek et al. 1997, Allan 2004). This global change is potentially creating widespread ecosystem simplification, loss of ecosystem services, and species extinctions (Tilman et al. 2001). Agricultural land uses influence stream ecosystems through multiple pathways including altered flows, degraded riparian habitats, and increased inputs of diffuse pollutants; changes which have been associated with detrimental effects on freshwater communities (Allan 2004). Degradation of water and habitat quality through inputs of fine inorganic sediment to streams, often associated with agricultural activities, is a widespread and pervasive problem (Walling 1990, Wood and Armitage 1997). Sediment influences have been associated with species losses, altered energy flow, and threshold impacts on community composition (Kemp et al. 2011, Jones et al. 2012, Burdon et al. 2013). However, the potentially important influences of sedimentation on stream food-web properties are less well understood.

Food webs represent a holistic systems approach to characterizing patterns of biodiversity and energy flow (Thompson et al. 2012). They typically describe interactions between consumers and resources (e.g., predator-prey interactions), helping to map community structure and function (Pimm et al. 1991). Food-web structure and dynamics may reflect underlying habitat conditions and strongly influence ecosystem processes (Ings et al. 2009), thus

providing a useful framework for understanding the effects of anthropogenic change (Woodward 2009). To gain new insights into food-web properties, increasingly sophisticated methods using stable isotopes and network analyses are being used (Layman et al. 2007, Stouffer 2010).

However, despite this, studies of food webs that use underlying environmental gradients remain rare, despite the opportunities they present in enabling us to disentangle causative relationships between changing habitat conditions and food-web structure and dynamics (Thompson et al. 2012).

Along gradients of deposited sediment, ‘bottom-up’ processes may affect energy flow and species distributions in stream ecosystems (Osmundson et al. 2002, Suttle et al. 2004), but sediment influences on food-web properties have rarely been documented. One of few studies to assess sediment impacts on trophic structure found simpler food webs, reflecting the loss of several important invertebrate functional-feeding groups in a tropical stream (Yule et al. 2010). Despite these changes to primary consumers, fish distribution and diets did not appear to change, thus indicating that food-chain length was less affected by sedimentation (Yule et al. 2010). Food-chain length (FCL) is a commonly used metric representing the vertical dimension of trophic architecture (Post 2002). We hypothesized that sedimentation could be associated with shorter food chains, reflecting predicted effects of environmental stress on resource availability and predatory invertebrates (Townsend et al. 1998, Anderson and Cabana 2009). The ‘resource availability’ hypothesis states that FCL should increase with greater basal production, because the maximum number of linkages in a food-web is constrained by energy transfer inefficiencies between trophic levels (Pimm 1982). Sedimentation may affect basal resource availability (Jones et al. 2012), and perturbations that act at the base of the food web can affect consumers in higher trophic levels (Petchey et al. 2004). In contrast, the dynamic constraints hypothesis posits that

higher consumers are rarer and more susceptible to the effects of disturbance, thus suggesting longer food chains are less persistent in model food webs (Pimm and Lawton 1977).

Perturbations that affect intermediate trophic levels may result in increased omnivory by higher predators, thus leading to shorter food chains (Post and Takimoto 2007, Anderson and Cabana 2009). We were also interested in the horizontal dimension (i.e., basal resource breadth) of trophic architecture. Deposited sediment homogenizes and degrades benthic habitat (Waters 1995), and we hypothesized that the effective resource breadth of stream food webs would contract with increasing sedimentation. We predicted that sediment deposition could strongly influence food-web resource breadth through habitat degradation and increased heterotrophy, potentially with an increased reliance on deposited fine particulate organic matter as a carbon source (Walters et al. 2007, Burdon et al. 2013).

Finally, we hypothesized that the combined influences of shortened food chains and resource breadth along a sedimentation gradient would be reflected in a ‘compression’ of trophic niche space (i.e., a reduction in trophic diversity). The trophic niche of an organism reflects consumer-resource interactions (Leibold 1995), and thus represents one dimension of Hutchinson’s (1957) ‘fundamental’ niche (i.e., the n-dimensional hypervolume). We used the ‘isotopic niche’ as a surrogate measure, since stable isotope ratios (typically carbon and nitrogen) obtained from an organism’s tissues derive from all trophic pathways culminating in that individual (Layman et al. 2007, Newsome et al. 2007). This has enabled stable isotope analysis (SIA) to be adopted as one of the main empirical tools in studying the trophic structure of food webs (Layman et al. 2012).

To test our three main three hypotheses, we used stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) obtained from aquatic communities in agricultural streams along a gradient of deposited

sediment. Quantitative measures derived from stable isotope data included maximum trophic position (Cabana and Rasmussen 1996) and the “community-wide” metrics of Layman et al. (2007) reformulated in a Bayesian statistical framework (Jackson et al. 2011). Secondly, using complementary community and ecosystem data, we sought to evaluate potential mechanisms contributing to the patterns documented by our main analyses. These included the proximate structural mechanisms affecting food-chain length (Post and Takimoto 2007), and four potential mechanisms affecting effective resource breadth as measured by the consumer $\delta^{13}\text{C}$ range: niche (a) partitioning, (b) generalists, (c) homogeneity, and (d) elimination (see Fig. 1 for further explanations).

METHODS

Study sites

We studied streams on the Canterbury Plains, located on the eastern side of New Zealand’s South Island. European settlement of the Plains since the 1840s has seen arable production (pasture, livestock, and cropping) become dominant (Haynes and Francis 1990), but prior to human settlement, this region comprised a mosaic of forest, shrublands, and wetlands (Wardle 1991). In the past three decades, widespread conversion to production-driven dairy farming has contributed to the agricultural intensification on the Plains (MacLeod and Moller 2006). For more details about riparian and surrounding vegetation, see Appendix A.1.

Twelve first to third order perennial streams were divided into six categories of dissolved nutrients and deposited sediment (i.e., a two by three factorial design incorporating differing levels of nutrients and sediment; for more information see Appendix A.2). Stream reaches were 30 m long; following the same length used by Thompson and Townsend (2005), and were

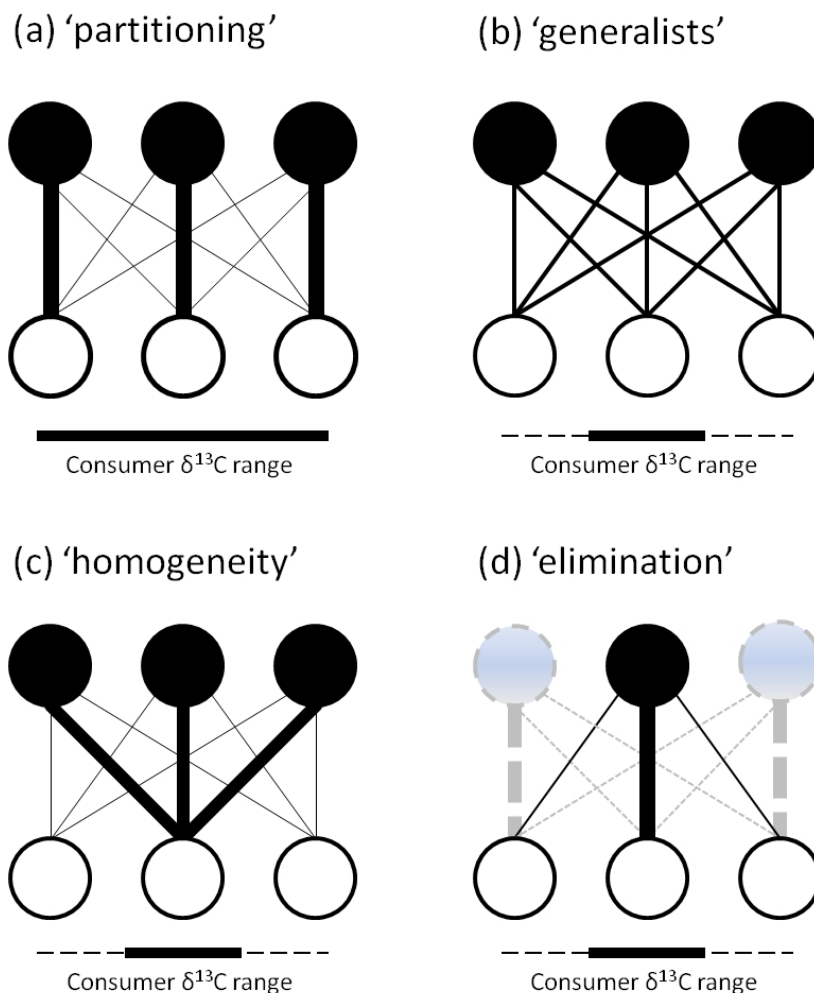


FIG. 1. Four hypothetical consumer-resource interactions that may influence niche breadth measured by the consumer $\delta^{13}\text{C}$ range (CR) in biological communities where resources show isotopic separation. (a) Specialized consumers (black circles) concentrate interactions (black lines) on separate resources (white circles) thus 'partitioning' niche space and leading to an expansion of CR. (b) Niche 'generalists' where consumers equally share resources, thus leading to a contraction of CR. (c) Niche 'homogeneity', where (i) specialized consumers concentrate interactions on a preferential resource or (ii) generalist consumers exploit an abundant resource; both leading to a contraction of CR. (d) Niche 'elimination' where environmental stress (i) removes specialist consumers (grey circles) and/or (ii) reduces favored resources below functionally viable levels, thus causing interactions to cease and leading to a contraction of CR. Niche processes (a)-(d) are not mutually exclusive, and all could occur simultaneously in real-world communities.

dominated by run-riffle sequences (pool habitat <2.5% of total channel area), with submerged macrophyte cover not exceeding 40%. Streams ranged from 2.5 – 6 m in width, and sites reflected the gentle slope of the Plains with an approximate gradient of 0.3%. Reaches were on separate tributaries and were sampled twice (fish communities were sampled on separate dates from habitat, resources, and invertebrates) during the austral summer (November 2009 to January 2010).

Data collection

Substrate composition and fine inorganic sediment were characterized at two different spatial scales (reach and patch) using multiple subjective (visual) and quantitative (physical) measures following the same methods used by Burdon et al. (2013). Using a semi-quantitative method, we visually estimated substrate composition and relative sediment cover at the patch scale (the area where quantitative invertebrate samples were collected; 0.0625 m^2 , $n=5$), and at the reach scale (0.09 m^2 quadrats randomly located throughout the 30-m study reach; $n=10$). Physical measurements of sediment included suspendable inorganic sediment (SIS, g/m^2 ; 0.07 m^2 , $n=15$), and sediment depth (mm, $n=10$); sampling locations were randomly distributed throughout the study reach. For further details regarding the collection and laboratory processing of sediment and other physicochemical data see Appendix A.3; collection and processing of basal resources are described in Appendix A.4.

To sample invertebrate communities quantitatively, five Surber samples (0.0625 m^2 , 250- μm mesh) were collected from the thalweg of the channel at evenly spaced locations. Additional composite kick-net samples (250- μm mesh) were collected to encompass all microhabitats (e.g., riffles, macrophytes, marginal vegetation, wood, and leaf litter) present in each study reach; invertebrate samples were placed on ice before being frozen. In the laboratory, thawed samples

were passed through a 500- μ m Endecott (Endecotts Limited, London, UK) sieve and all invertebrates removed, identified, and counted to the lowest practicable level (usually genus) using invertebrate identification guides. Taxa presence data from kick-nets were combined with data recorded from the Surber samples to create qualitative response variables (e.g., taxa richness) at the reach scale. For further information about invertebrate indices and trait analyses see Appendix A.5.

Fishes and decapod crustaceans were sampled using quantitative or qualitative electro-fishing techniques to estimate species richness and obtain specimens for stable isotopes analysis (SIA). The upper and lower ends of each study reach were blocked with nets, and as many fish as possible were removed during three successive electro-fishing passes; we conducted single-pass electro-fishing focusing on optimal fish habitats in study reaches where turbidity caused by suspended sediment made quantitative electro-fishing untenable. All electro-fishing was conducted using a backpack electric-fishing machine (Kainga EFM 300, NIWA Instrument Systems, Christchurch, NZ) which was operated with pulsed DC current (200–400 V). Fishes retained from each site for SIA were euthanized with a lethal dose of 2-phenoxyethanol, placed immediately on ice, and then frozen until laboratory processing.

Stable isotope sampling and analysis

Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis was conducted on consumers and basal resources to assess changes to trophic structure and food webs along the sedimentation gradient. After thawing in the laboratory, composite kicknet samples were passed through a 500- μ m sieve and stream invertebrates removed for isotopic analysis according to two criteria: taxa that were abundant (i.e., ≥ 100 individuals present in samples) and/or large bodied (i.e., > 5 mm body length); thus potentially contributing disproportionately to overall biomass. For the large-bodied

taxa, individuals provided sufficient material for analysis, but for smaller specimens (e.g., most chironomid larvae), numerous individuals were pooled. Stomach contents were removed from predatory invertebrates prior to drying (Jardine et al. 2005). All fish taxa recorded from study streams were used, with one exception; the sole female long-fin eel (*Anguilla dieffenbachii*) collected at Waihikuawa Stream was not euthanized because this is a threatened species that can live for ~80 years. Where possible, three specimens of each species were collected to adequately characterize the range of sizes present at sites; dorsal muscle tissue was removed from thawed individuals for SIA.

To estimate isotopic content, samples of basal resources, invertebrates, and fish were dried (60 °C, 48 hours) and ground into a fine powder using a ceramic mortar and pestle. Subsamples from individuals and aggregates of small-bodied invertebrate taxa (~1.0 mg) and basal resources (~2.0 mg) were then encapsulated into 8 x 5 mm tin capsules (OEA Laboratories Ltd., Cornwall, UK), and sent to the Stable Isotope Facility (University of California, Davis, CA, USA), where they were analyzed on a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotope ratios, R (i.e., $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$), were estimated relative to the ratios of their respective standards (Pee Dee Belemnite limestone and atmospheric nitrogen) and are expressed in per mille delta notation (Eq. 1):

$$\delta^1 = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} + 1 \right] \times 1000 \quad (1)$$

where δ^1 is either ^{13}C or ^{15}N , and R is the ratio of either one to the respective lighter isotope (^{12}C or ^{14}N). The analytical error (i.e., 1 SD of the lab standard) associated with our $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sample runs was estimated at 0.11 ‰ ($\delta^{13}\text{C}$) and 0.11 ‰ ($\delta^{15}\text{N}$) for the invertebrates, and 0.04 ‰

($\delta^{13}\text{C}$) and 0.07 ‰ ($\delta^{15}\text{N}$) for the fish. Prior to data analysis, we corrected $\delta^{13}\text{C}$ signatures for lipid content using observed C:N ratios and a published empirical relationship (Post et al. 2007).

We estimated food-chain length (FCL) at each site following the maximum trophic position (MTP) convention. As $\delta^{15}\text{N}$ of basal resources (e.g., periphyton, detritus, etc.) is prone to considerable variation, primary consumers are commonly used to calculate baseline correction factors (Cabana and Rasmussen 1996, Rybczynski et al. 2008). Therefore, we calculated primary consumer $\delta^{15}\text{N}$ as the mean $\delta^{15}\text{N}$ of three ubiquitous invertebrates, a leptophlebiid mayfly *Deleatidium*, a conoesucid caddisfly *Pycnocentroides*, and the amphipod *Paracalliope fluviatilis*. At sites where these primary consumers were absent, suitable alternative taxa were used (Appendix B). Stable isotope analysis (SIA) derived trophic position (TP) of individual fish was estimated following (Cabana and Rasmussen 1996) as (Eq. 2):

$$\text{TP} = \left[\frac{\text{fish } \delta^{15}\text{N} - \text{primary consumer } \delta^{15}\text{N}}{3.4 \text{ ‰}} \right] + 2 \quad (2)$$

The mean fractionation rate was assumed to be 3.4 ‰ per trophic transfer (Post 2002). While this rate does not apply universally, independent diet-based validations suggest that TP can be accurately estimated for fishes using SIA (Vander Zanden et al. 1997, Rybczynski et al. 2008).

To further analyze trophic structure, we used six “community-wide” isotopic metrics that reflect components of trophic architecture (Layman et al. 2007). The first four measure the total extent of spacing within $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space, thus representing community-wide measures of trophic diversity (Table 1). The final two metrics reflect the relative position of species to each other within niche space (Table 1). An additional measure of trophic diversity was calculated using standard ellipse area; an approach that is less susceptible to the effects of sample size and

TABLE 1. Description of metrics used to describe stream communities using consumer stable isotope bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Metric name	Metric abbrev.	Bayesian version	Description	Reference
$\delta^{15}\text{N}$ range	NR	NR.B	An indication of vertical trophic diversity	
$\delta^{13}\text{C}$ range	CR	CR.B	An indicator of niche diversification at the base of the food web	
Trophic area	TA	THA.B	Total convex hull area encompassed by all species in bi-plot space, thus measuring the total amount of niche space occupied	Layman et al. 2007
Centroid distance	CD	CD.B	Average Euclidean distance of each species to the bi-plot centroid, thus representing another measure of trophic diversity	
Nearest neighbor distance	NND	NND.B	The mean Euclidean distance between each species in the bi-plot, thus representing the overall density of species packing	
Standard deviation of NND	SDNND	SDNND.B	The evenness of species packing in the bi-plot space	
Standard ellipse area	SEA	SEA.B	Standard ellipse area encompassed by all species or individuals in bi-plot space, thus measuring the total amount of niche space occupied	Jackson et al. 2011

extreme values (Jackson et al. 2011). The ammocoetes and/or macrophthalmia of the lamprey *Geotria australis* (Geotriidae) present at two sites (Waihikuawa and Northbrook) were excluded from the calculation of fish isotopic metrics. Lamprey occupied an area of isotopic niche-space indicating specialized feeding on detritus, thus were very different trophically from the other New Zealand fish species which are mostly predatory, feeding on invertebrates and other fish (McIntosh 2000). We used a Bayesian statistical framework (Jackson et al. 2011) to help mitigate the shortcomings of the Layman metrics (Newsome et al. 2007, Hoetinghaus and Zeug

2008). We calculated Layman metrics and standard ellipse areas from consumer isotope data using the “siar” package in R; following Bayesian inference techniques, mean values were extracted from 10,000 posterior draws (Parnell and Jackson 2011).

A Bayesian statistical framework was used to estimate the relative contributions of detritus and periphyton to the diets of primary consumers using two-isotope, two-source mixing models (Parnell et al. 2010). No prior assumptions were made about enrichment values (Parnell et al. 2010); mixing models were calculated using the “siar” package in R (Parnell and Jackson 2011). This analysis uses a Markov chain Monte Carlo (MCMC) for normally distributed data with a dirichlet mixture mean to estimate relative dietary proportions; mean values were extracted from 20,000 iterations.

Data analysis

Principal components analysis (PCA) in R (R Development Core Team 2010) was used to assess the influence of physico-chemical parameters other than sediment and nutrients on study characteristics. To test these differences according to sediment cover categories (i.e., ‘low’, ‘medium’, and ‘high’), ANOSIM (Analysis of Similarity) was conducted using the “adonis” command in the R package ‘vegan’ (Oksanen et al. 2010). A meta-NMDS (Non-Metric Dimensional Scaling) analysis was performed using an Euclidean distance matrix and analysis of variance conducted using a permutation test (1,000 iterations) with pseudo-*F* ratios (Oksanen et al. 2010). PCA was also used to reduce our measures of deposited fine sediment into a single index (Axis 1 scores; PC1 henceforth, Appendix D Table 1). To enable model parameterization of PC1 and make results more intuitive, a constant (3) was added to each score to transform negative values to positive figures. Where appropriate, data were transformed to meet assumptions of analyses and improve heteroscedasticity (e.g., SIS, sediment depth, nitrate, and

DRP were log-transformed [$\log_{10}(x + 1)$]). Variables were centered (subtracted from sample means) and scaled (divided by sample standard deviation) for analyses requiring standardized data. Pearson's product-moment correlations in R (R Development Core Team 2010) were used to assess relationships between physico-chemical variables.

Community composition data were analyzed to better explain possible proximate changes influencing the food web metrics measured by stable isotopes analysis. Fish community presence-absence data (occupancy), square-root transformed invertebrate community abundances (individuals/0.0625 m²), invertebrate occupancy data, and SIA invertebrate data were analyzed using Bray-Curtis similarity matrices with non-metric multi-dimensional scaling (NMDS) in Primer. Pearson's product-moment correlations of the NMDS Axis 1 scores were used to compare the similarity of different community data sets and their respective relationships to sediment (PC1). Invertebrate taxa richness indices were rarefied using the "vegan" package in R (Oksanen et al. 2010); rarefied richness was calculated for 200 individuals. The joint and independent contribution of sediment and nutrients to community composition was assessed using partial redundancy analyses; see Appendix C.1.

The joint and independent effects of environmental determinants on maximum trophic position were tested using hierarchical partitioning; see Appendix C.2. To assess the shape and significance of the relationship between deposited sediment and stream response variables, regression models were selected using an information-theoretic approach (Burnham and Anderson 2002) in conjunction with traditional regression analysis techniques. Appendix C.3 summarizes these methods and provides the rationale for excluding outlying sites. Models were fitted using the "lm" and "nls" commands in R, and the lowest Akaike Information Criterion (AIC_c) values calculated to identify the best-fitting model (Appendix C.3). The change in AIC_c

(i.e., ΔAIC_c) between the preferred model and the next closest is provided as a goodness of fit measure where more than one regression model (i.e., non-linear regression) has been tested for the same data (Appendix C Tables 1-3); in most instances, parameter estimates (± 1 standard error) and tests of significance ($\alpha = 0.05$) are provided in the figure captions. For consistency, F -statistics and R^2 values are reported on all regression figures.

RESULTS

Sediment and physico-chemical variables

Physico-chemical and biotic parameters for the twelve streams were variable, particularly for sediment and dissolved nutrients (Table 2). Principal Components Analysis (PCA) showed differing influences of physico-chemical variables other than sediment and nutrients on sites (Fig. 2a), where PC1 explained 40% of total variance (Appendix D Table 1). However, Analysis of Similarity (ANOSIM) using sediment cover categories showed that overall, sites in these groups were not significantly different physico-chemically ($F_{2,9} = 0.93$, $R^2 = 0.17$, $P = 0.53$, Fig. 2b), other than the differences in deposited sediment and dissolved nutrients. Deposited sediment measurements (cover, depth, and volume) were colinear, and PCA reduced these measures into a single index (PC1) accounting for 85.0% of total variance (Appendix D Table 1). This combined sediment metric (PC1) was not significantly correlated with dissolved nitrate (Pearson's Product-Moment correlation, $r = 0.252$, $P = 0.429$), dissolved reactive phosphorus (DRP; $r = -0.016$, $P = 0.962$), water temperature ($r = -0.016$, $P = 0.961$), or dissolved oxygen ($r = -0.363$, $P = 0.246$); but sediment (PC1) was correlated to mean stream flow velocity ($r = -0.654$, $P < 0.05$) and flow variance ($r = -0.644$, $P < 0.05$). Nitrate and DRP were not significantly correlated ($r = 0.278$, $P = 0.379$) and ecosystem size (e.g., stream width and cross-sectional area) was not correlated with any other physico-chemical variable.

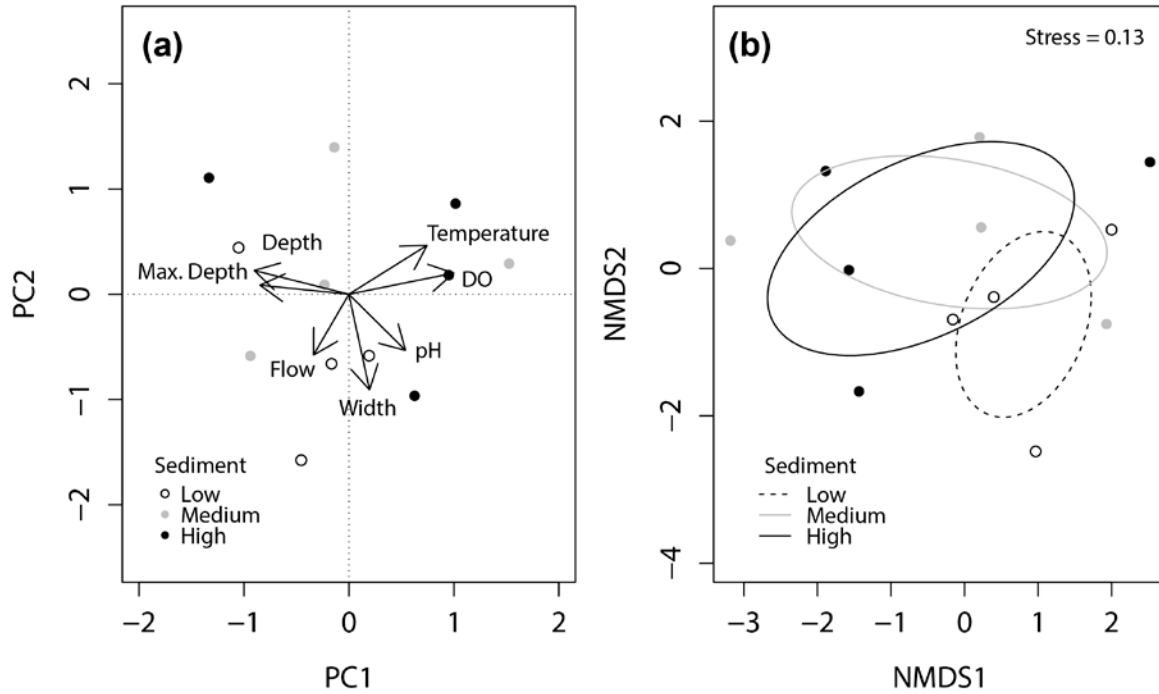


FIG. 2. Results from a) Principal Components Analysis (PCA) showing influences of physico-chemical variables (excluding sediment and nutrients) on study sites grouped by % fine sediment cover (see Methods section) and b) Non-Metric Dimensional Scaling (NMDS) showing the dissimilarity of sites grouped by the sediment cover categories; standard error ellipses show the variability of each group. Max. depth, maximum depth; DO, dissolved oxygen (mg/L).

Isotopic community metrics

Sediment (PC1) had a negative influence on effective basal resource niche breadth. Total community (all consumers), fish, and invertebrates all had a narrowing Bayesian consumer $\delta^{13}\text{C}$ carbon range (CR.B) with increasing sediment. Both total community carbon range (Linear regression [LR], $F_{1,9} = 9.07$, $P < 0.05$, $R^2 = 0.476$) and invertebrate carbon range (Fig. 3a) were negatively associated with increased sediment. This reduction in effective basal resource breadth contributed to decreased trophic diversity as deposited sediment increased along the gradient. Sediment was negatively associated with total community trophic diversity (trophic area, TA), as

TABLE 2. Physico-chemical characteristics of 12 streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Fine sediment cover was assessed at two different spatial scales; only reach-scale (30 m) data is presented here. SIS, suspendable inorganic sediment; PC1, Principal components analysis (PCA) Axis 1 scores of sediment measures [+ constant (3)]; CSA, cross-sectional area; SC, specific conductivity ($\mu\text{S}_{25^\circ\text{C}}/\text{cm}$); DRP, dissolved reactive phosphorus.

Stream	Latitude (°N)	Longitude (°S)	Fine sediment				Physical				Chemical		
			% cover	SIS (g/m ²)	Depth (mm)	PC1	Velocity (m/s)	Width (m)	Depth (m)	CSA (m ²)	SC ($\mu\text{S}/\text{cm}$)	NO ₃ -N (mg/l)	DRP ($\mu\text{g}/\text{l}$)
Clearwater	-43.447	172.581	13	151	8	2.01	0.39	3.4	0.19	0.64	75	0.50	2.9
Cridges	-43.469	172.549	8	45	2	1.24	0.26	4.3	0.28	1.20	74	0.30	36.1
Southbrook	-43.323	172.592	4	12	0.3	0.61	0.14	2.8	0.38	1.07	115	1.43	11.6
Cust	-43.346	172.563	1	48	0.3	0.94	0.43	5.9	0.14	0.84	182	5.46	11.8
Waihikuawa	-43.435	172.585	19	244	1	1.88	0.30	3.2	0.13	0.40	71	0.31	6.7
Northbrook	-43.314	172.613	18	392	9	2.48	0.42	3.2	0.33	1.07	97	0.36	2.6
Saltwater	-43.257	172.669	21	534	6	2.51	0.33	3.6	0.16	0.58	113	0.42	10.8
Flaxton	-43.340	172.602	42	175	14	3.17	0.17	2.5	0.18	0.46	146	2.03	18.0
Shipleys	-43.459	172.566	76	814	72	4.65	0.06	5.4	0.21	1.13	71	0.14	6.3
Springs	-43.655	172.482	100	355	72	5.54	0.15	4.0	0.17	0.69	106	1.76	11.7
Easterbrook	-43.329	172.578	90	892	63	5.28	0.03	3.5	0.14	0.50	138	2.25	15.7
Courtenay	-43.413	172.630	83	4,480	317	5.69	0.20	3.0	0.32	0.95	185	5.21	9.5

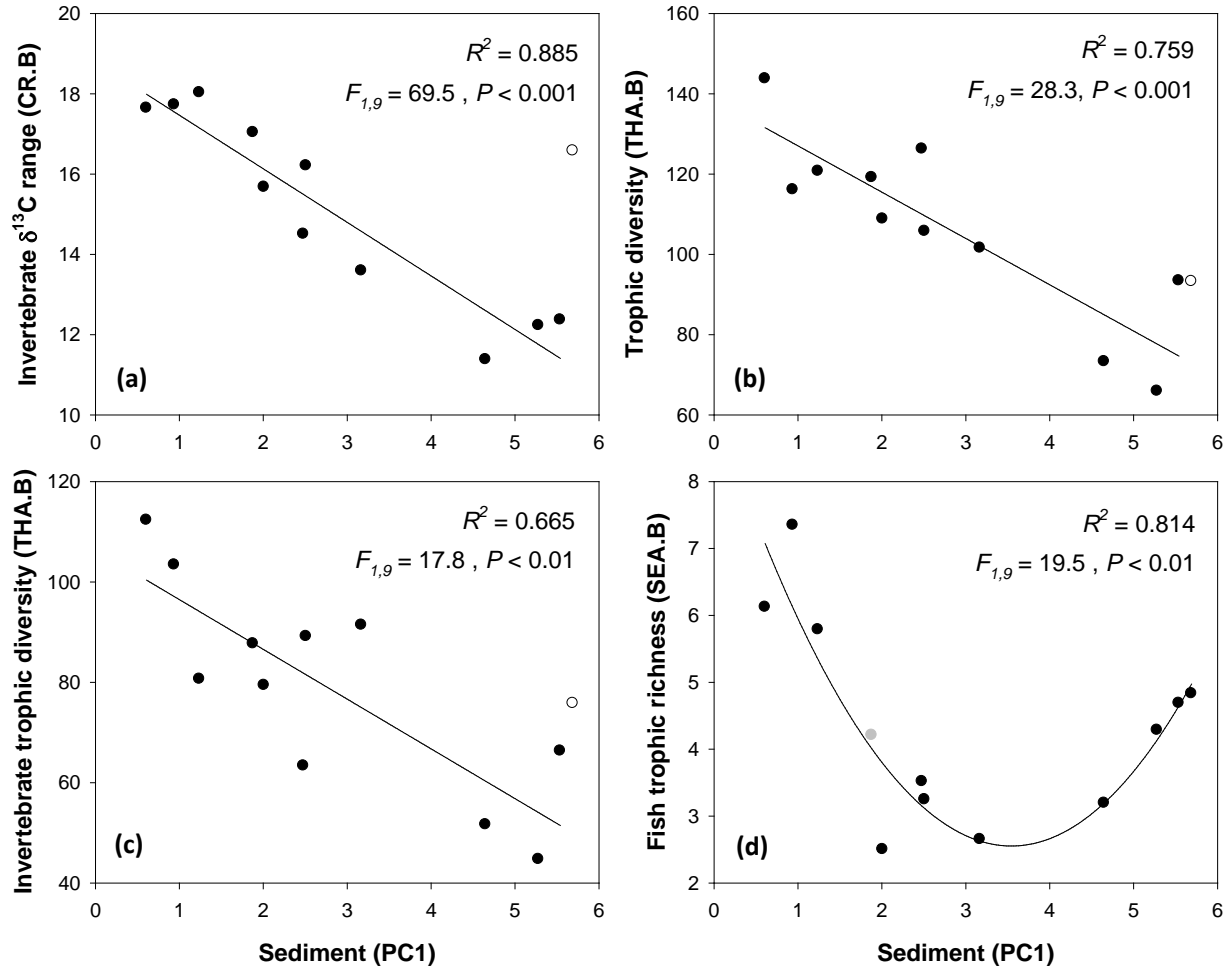


FIG. 3. Results from community stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) metrics of twelve streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Linear relationship (LR) between deposited sediment (PC1) and (a) invertebrate $\delta^{13}\text{C}$ range (CR.B) where $y = a + bx$ had parameter estimates, $a = 18.8 \pm 5.1$ ($P < 0.001$), $b = -1.33 \pm 0.16$ ($P < 0.001$); the open circle shows an outlying site (Courtenay), see Appendix C.3, (b) total (fish and invertebrates) trophic diversity (THA.B), $y = a + bx$, $a = 138.6 \pm 7.0$ ($P < 0.001$), $b = -11.5 \pm 2.2$ ($P < 0.001$), (c) invertebrate trophic diversity (THA.B), $y = a + bx$, $a = 106.4 \pm 7.5$ ($P < 0.001$), $b = 9.92 \pm 2.35$ ($P < 0.01$), and (d) quadratic relationship between sediment (PC1) and fish trophic diversity (SEA.B) where $y = a + bx + cx^2$, with $a = 9.15 \pm 0.84$ ($P < 0.001$), $b = -3.72 \pm 0.64$ ($P < 0.001$), $c = 0.53 \pm 0.10$ ($P < 0.001$). The grey circle indicates an outlying site (Waihikuawa), see Appendix C.3.

measured by the Bayesian total hull area (THA.B; Fig. 3b) and the Bayesian standard ellipse area (SEA.B; LR, $F_{1,10} = 9.80$, $P < 0.05$, $R^2 = 0.495$). This result closely mirrored the influence of sediment on invertebrate trophic diversity, where both THA.B (Fig. 3c) and SEA.B (LR, $F_{1,10} = 10.3$, $P < 0.01$, $R^2 = 0.509$) declined in association with increasing levels of deposited sediment. No other total community or invertebrate SIA metrics were significantly associated with sediment.

In contrast, both fish community CR.B (Fig. 4a) and NR.B (Fig. 4b) declined with sediment. Although the presence of only two fish taxa at two sites invalidated the use of the trophic hull method (THA.B), using species means showed fish community trophic diversity (SEA.B) had a ‘U-shaped’ relationship with increasing sediment (NLR, $\Delta AIC_c = -13.9$, Fig. 3d), and an identical pattern was observed using individual fish isotope data ((NLR, $\Delta AIC_c = -13.5$, Fig. 4c). This was likely due to a reduction in species packing (NND.B) at low and high sediment sites, leading to a similarly ‘U-shaped’ relationship with increasing sediment (NLR, $\Delta AIC_c = -6.70$; Fig. 4d).

Trophic position and food-chain length

However, increasing deposited sediment was not associated with a decrease in food-chain length (FCL). Multiple regression analysis using hierarchical partitioning revealed that sediment and ecosystem size had no significant influence on maximum trophic position (MTP); only dissolved reactive phosphorus (DRP) was significantly associated with MTP (Hierarchical partitioning, Z-score = 2.66, Fig. 5a), with an apparent positive influence on FCL (Fig. 5b). A potential proximate driver of this pattern was predator body size; the maximum length of the short-fin eel (*Anguilla australis*) was significantly correlated with both phosphorus ($r = 0.66$, $P < 0.05$) and MTP ($r = 0.60$, $P < 0.05$).

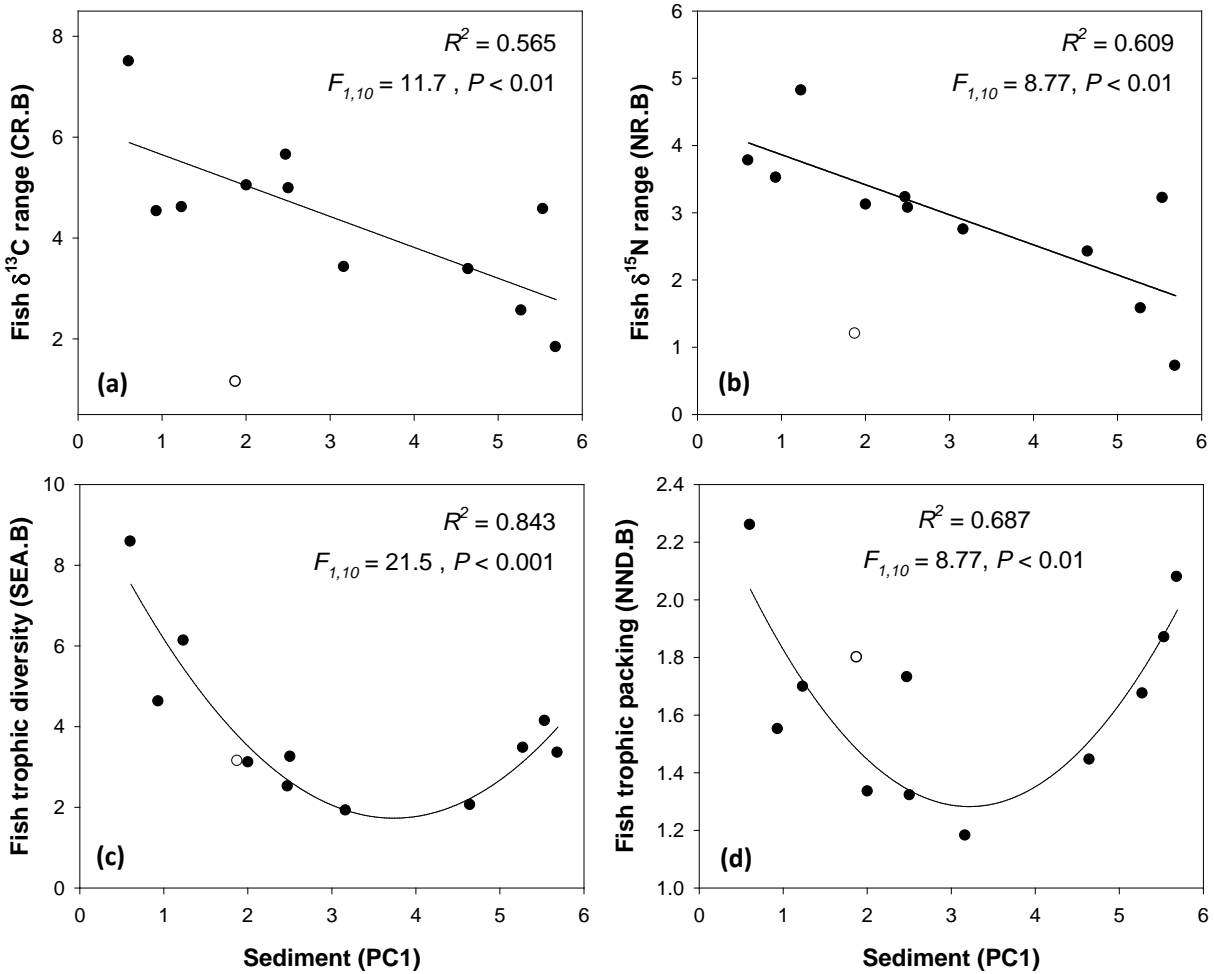


FIG. 4. Results from fish community stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) metrics of 12 streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Linear relationship (LR) between deposited sediment (PC1) and (a) fish $\delta^{13}\text{C}$ range (CR.B) where $y = a + bx$ had parameter estimates $a = 6.26 \pm 0.44$ ($P < 0.001$) and $b = -0.61 \pm 0.18$ ($P < 0.01$), (b) fish $\delta^{15}\text{N}$ range (CR.B), $y = a + bx$, $a = 4.31 \pm 0.43$ ($P < 0.001$), $b = -0.45 \pm 0.12$ ($P < 0.01$). Quadratic relationship between sediment (PC1) and (c) and fish individual trophic diversity (SEA.B) where $y = a + bx + cx^2$, with $a = 10.0 \pm 0.97$ ($P < 0.001$), $b = -4.43 \pm 0.74$ ($P < 0.001$), $c = 0.59 \pm 0.11$ ($P < 0.001$) and (d) fish species mean nearest neighbor distance (NND.B), $y = a + bx + cx^2$, $a = 2.43 \pm 0.23$ ($P < 0.001$), $b = -0.71 \pm 0.18$ ($P < 0.01$), $c = 0.11 \pm 0.03$ ($P < 0.01$). The open circle shows an outlying site (Waihikuawa); see Appendix C.3.

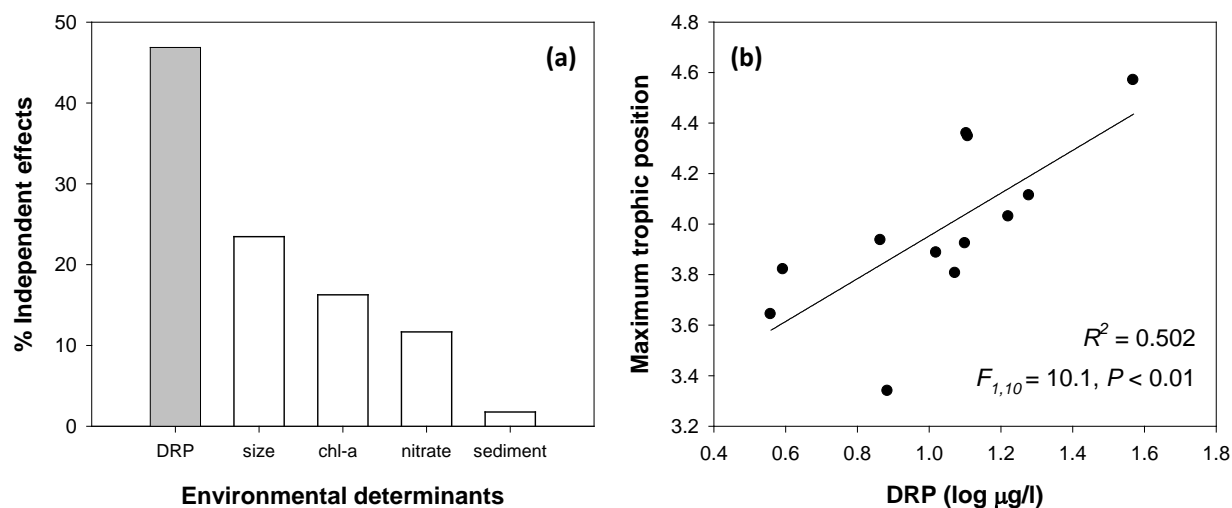


FIG. 5. Results from maximum trophic position (MTP) analyses of fish communities across a deposited sediment gradient in 12 streams sampled on the Canterbury Plains, South Island during the summer of 2009-2010. (a) Hierarchical partitioning of environmental determinants contributing to food chain length (i.e., MTP); and (b) linear regression of dissolved reactive phosphorus and maximum trophic position where $y = a + bx$, $a = 3.1 \pm 0.3$ ($P < 0.001$), $b = 0.9 \pm 0.3$ ($P < 0.01$). DRP, dissolved reactive phosphorus; size, mean stream width (m); chl-a, chlorophyll-a concentration ($\mu\text{g}/\text{cm}^2$); nitrate, $\text{NO}_3\text{-N}$ mg/l; sediment, principal components analysis Axis 1 scores (PC1) of deposited sediment measures.

Community diversity and composition

Deposited sediment strongly affected faunal diversity and invertebrate community composition. Total community richness (NLR, $\Delta\text{AIC}_c = -2.55$) and invertebrate community richness (NLR, $\Delta\text{AIC}_c = -2.22$, Fig. 6a) both demonstrated a negative ‘hockey-stick’ shaped relationship with deposited sediment. Importantly, however, there was no significant change in the taxa richness of invertebrates used for stable isotopes analysis (SIA) along the sediment gradient; nor did the relative proportion of taxa used significantly change. The Layman metrics

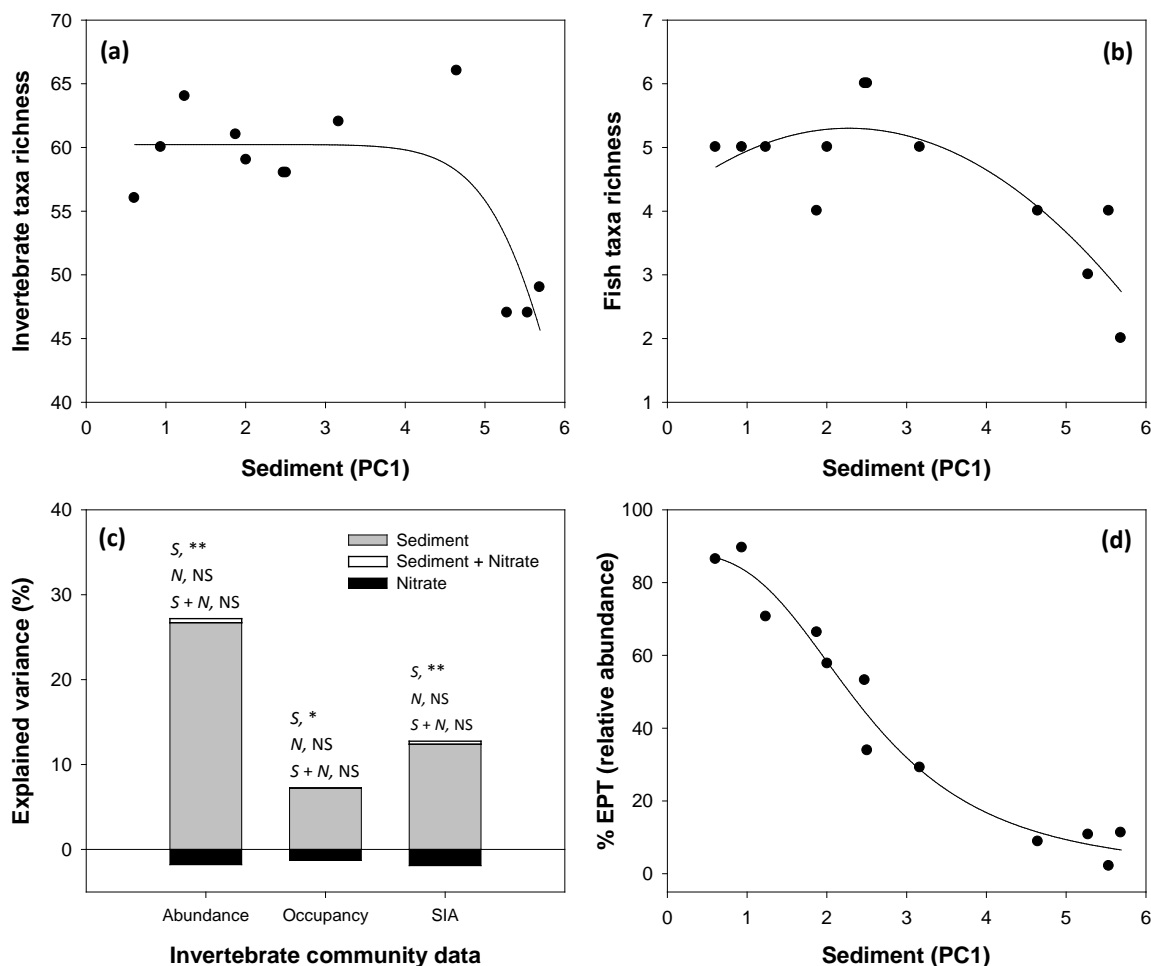


FIG. 6. Results from community analyses of 12 streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. (a) 3-parameter logistic relationship (NLR) between deposited sediment (PC1) and invertebrate taxa richness where $y = a/[1 + (x/b)^c]$ with $a = 60.2 \pm 1.5$ ($P < 0.001$), $b = 6.32 \pm 0.59$ ($P < 0.001$), $c = 10.8 \pm 7.8$ ($P = 0.20$). (b) fish taxa richness, $y = a + bx + cx^2$, with $a = 4.16 \pm 0.80$ ($P < 0.001$), $b = 1.00 \pm 0.60$ ($P = 0.13$), $c = -0.22 \pm 0.09$ ($P < 0.05$). (c) *p*RDA result testing the joint and independent effects (% explained variance) of sediment and nitrate on invertebrate community data. Abundance, individuals/0.0625 m²; occupancy, presence-absence; SIA, invertebrates (occupancy) selected for stable isotopes analysis. (d) 3-parameter logistic relationship between sediment (PC1) and EPT % where $y = a/[1 + (x/b)^c]$ with $a = 88.0 \pm 5.20$ ($P < 0.001$), $b = 2.50 \pm 0.16$ ($P < 0.001$), $c = 3.06 \pm 0.50$ ($P < 0.001$); EPT, sediment-sensitive aquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera.

can be affected by the number of taxa sampled (Jackson et al. 2011). Fish community richness showed a ‘hump-backed’ relationship with sediment (NLR, $\Delta AIC_c = -1.35$, Fig. 6b); but neither sediment nor nutrients significantly explained fish community occupancy data using *p*RDA.

Total invertebrate community abundance and occupancy data, and the invertebrates selected for SIA, were all strongly correlated with using the Axis 1 scores from non-metric dimensional scaling (NMDS) analyzes (Appendix D Table 2). In turn, these invertebrate metrics were all strongly correlated with deposited sediment (PC1). Sediment alone significantly explained invertebrate community composition patterns, whereas the joint and independent contribution of nitrate had no significant influence (*p*RDA, Fig. 6c). Similar results were observed where nitrate was replaced by dissolved reactive phosphorous (DRP) or analyzed together with DRP. Much of the change in invertebrate community composition was driven by reduced abundances of sediment-sensitive EPT taxa (Ephemeroptera, Plecoptera, Trichoptera). EPT richness at the reach scale significantly declined with increasing sediment (LR, $F_{1,10} = 20.5$, $P < 0.01$, $R^2 = 0.672$), but rarefied richness calculated from abundance data showed no significant change. Similar patterns were observed with total invertebrate taxa richness. This suggested that much of the decline in EPT richness was attributable to reduced abundances. In contrast, relative abundance significantly declined with sediment (NLR, $\Delta AIC_c = -2.66$, Fig. 6d).

Deposited sediment was associated with changes in invertebrate community feeding traits including functional-feeding groups (FFGs). Using community abundance data, the trait frequency of ‘grazers’ (LR, $F_{1,10} = 18.0$, $P < 0.01$, $R^2 = 0.643$) and ‘shredders’ (LR, $F_{1,10} = 31.4$, $P < 0.001$, $R^2 = 0.758$) significantly decreased with sediment (Fig. 7a,b); similarly, significant associations were seen with total occupancy data and the invertebrates selected for SIA. Although the trait frequency of ‘collectors’ did not significantly change with sediment, the trait

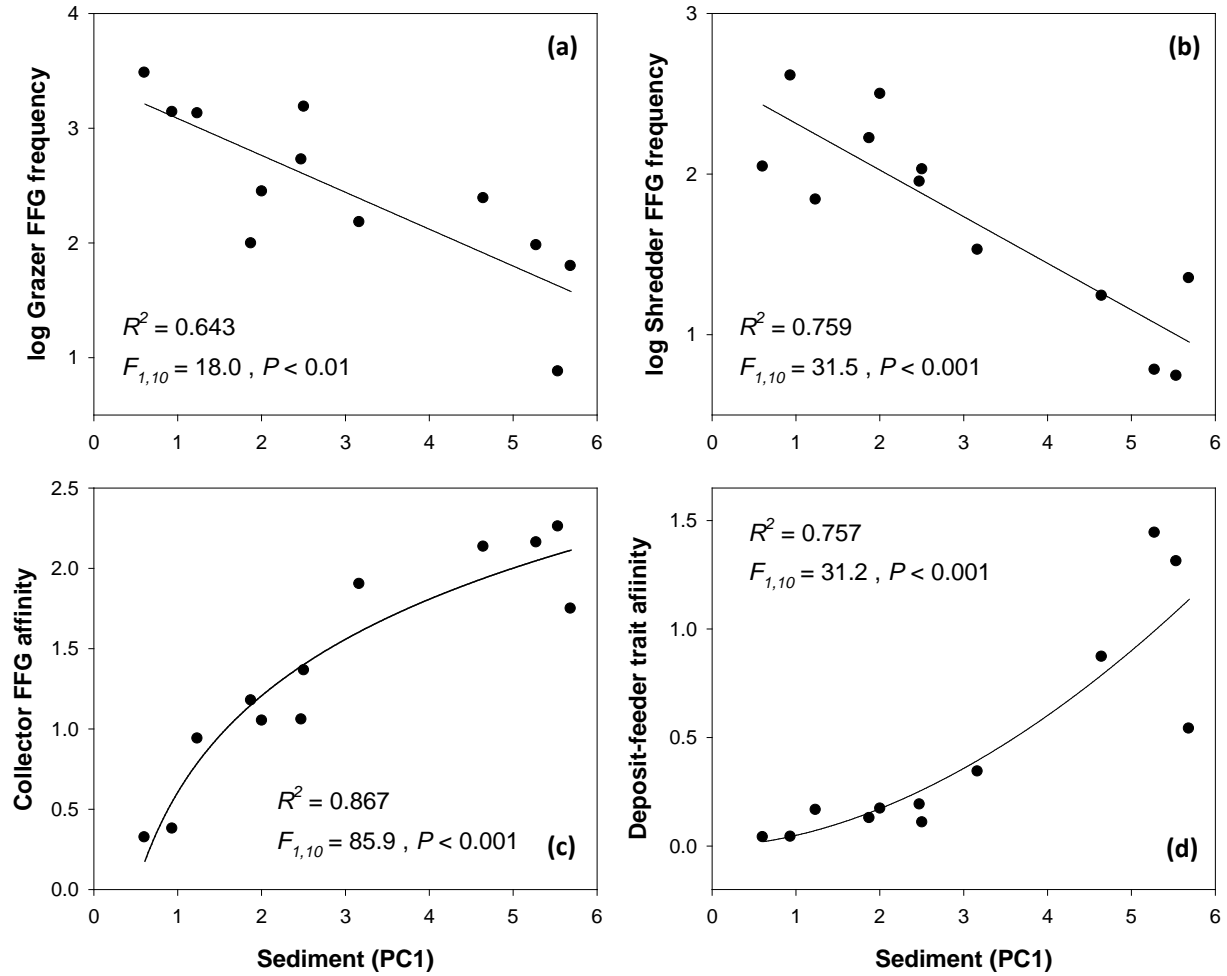


FIG. 7. Results of invertebrate community feeding-trait analyses from twelve streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Linear relationship between deposited sediment (PC1) and: (a) \log_{10} 'grazer' functional-feeding group (FFG) frequency where $y = a + bx$ had parameter estimates $a = 3.4 \pm 0.3$ ($P < 0.001$), $b = -0.32 \pm 0.08$ ($P < 0.01$); (b) \log_{10} 'shredder' FFG frequency, $y = a + bx$, $a = 2.61 \pm 0.18$ ($P = 0.001$), $b = -0.29 \pm 0.05$ ($P < 0.001$). (c) Logarithmic relationship between sediment (PC1) and 'collector' FFG affinity (FFG trait frequency per individual), $y = a + b\ln(x)$, $a = 0.60 \pm 0.11$ ($P < 0.001$), $b = 0.87 \pm 0.09$ ($P < 0.001$). (d) Exponential relationship between sediment (PC1) and 'deposit-feeder' trait affinity where $y = ax^b$, with $a = 0.60 \pm 0.11$ ($P < 0.001$), $b = 0.87 \pm 0.09$ ($P < 0.001$).

affinity (mean trait score per individual) increased asymptotically (NLR, $\Delta AIC_c = -2.21$, Fig. 7c). Similarly, significant linear increases in ‘collector’ trait affinity (per taxon) were seen in total occupancy data (LR, $F_{1,10} = 9.01$, $P < 0.05$, $R^2 = 0.474$) and the SIA taxa (LR, $F_{1,10} = 9.12$, $P < 0.05$, $R^2 = 0.477$). Based on abundance data, the trait frequency (LR, $F_{1,10} = 13.9$, $P < 0.01$, $R^2 = 0.582$) and affinity (NLR, $\Delta AIC_c = -1.04$, Fig. 7d) of invertebrates associated with deposit-feeding increased with sedimentation; similar patterns were seen in the occupancy data. This contrasted linear declines in taxa associated with rheophilic habitat; see Appendix D Table 3 for a summary of all feeding-trait results.

Basal resources availability and quality

An increase in deposited sediment was associated with other changes at the ecosystem level. The biomass (AFDM g/m²) of fine benthic organic matter (FPOM) increased with total sediment mass (Fig. 8a), whereas chlorophyll-*a* concentrations (µg/cm²) and the biomass (AFDM g/m²) of coarse particulate organic matter (CPOM) did not change significantly. This meant the ratio of chlorophyll-*a* to FBOM, and CPOM to FBOM, both decreased with increased sedimentation (Homogeneity of lines test, $t_{1,20} = 0.80$, $P = 0.44$, Fig. 8b). Isotopic mixing model analyses of primary consumers indicated that the relative contribution of periphyton to invertebrate diets decreased with increasing sedimentation (LR, $F_{1,10} = 82.6$, $P < 0.001$, $R^2 = 0.892$). The relative contribution of periphyton decreased for ‘collectors’ (Fig. 8c) and ‘grazers’ (LR, $F_{1,10} = 27.9$, $P < 0.001$, $R^2 = 0.736$), but not ‘shredders’. The quality of periphyton resources decreased with sedimentation as indicated by an asymptotic increase in the ratio of carbon to nitrogen (NLR, $\Delta AIC_c = -3.85$, Fig. 8d); a significant increase in C:N was also observed for FBOM (LR, $F_{1,10} = 4.99$, $P < 0.05$, $R^2 = 0.333$), but no change was observed for suspended fine particulate matter (SFPM) or CPOM.

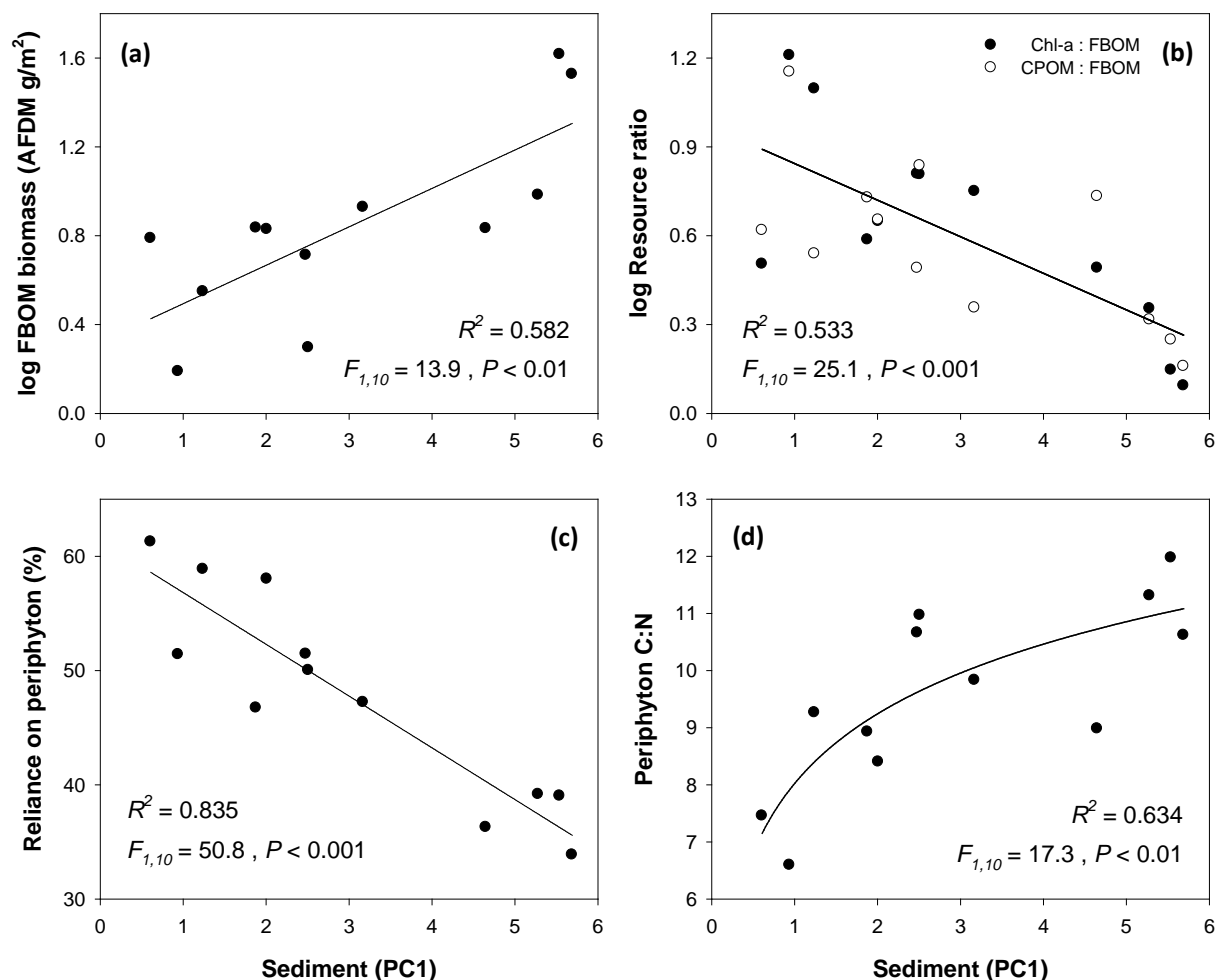


FIG. 8. Results from analyses of basal resources and invertebrate consumers collected from twelve streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Linear relationship between deposited sediment (PC1) and: (a) $\log_{10}(x + 1)$ fine benthic organic matter (FBOM; ash-free dry mass g/m²) where $y = a + bx$ had parameter estimates $a = 0.32 \pm 0.16$ ($P = 0.07$), $b = 0.017 \pm 0.05$ ($P < 0.01$); (b) $\log_{10}(x + 1)$ ratio of chlorophyll-a concentrations (mg/l) and coarse-particulate organic matter (CPOM; ash-free dry mass g/m²) to FBOM, $y = a + bx$, $a = 0.97 \pm 0.09$ ($P < 0.001$), $b = -0.12 \pm 0.02$ ($P < 0.001$); (c) mean dietary contribution of periphyton to ‘collector’ invertebrates, $y = a + bx$, $a = 61.4 \pm 2.2$ ($P < 0.001$), $b = -4.53 \pm 0.48$ ($P < 0.001$); and (d) periphyton resource quality (molar C:N), $y = a + b \ln(x)$, with $a = 8.02 \pm 0.48$ ($P < 0.001$), $b = 1.76 \pm 0.42$ ($P < 0.001$)

DISCUSSION

Studies of food webs that use underlying environmental gradients are crucial to helping disentangle causative relationships between changing habitat conditions and food-web structure and dynamics (Thompson et al. 2012). Our results show strong evidence that ecosystem and community changes associated with deposited sediment influenced the ‘compression’ of isotopic niche space in stream food webs, and that much of this shift was attributable to a contraction of the consumer $\delta^{13}\text{C}$ range. In contrast, sediment did not explain variation in the maximum trophic position (e.g., food-chain length). Although ecologists have long sought to identify determinants of food-chain length, much less research effort has been invested in understanding changes among other food-web properties across shifting environmental conditions (Tunney et al. 2012). Our results indicate changes in other food-web properties associated with environmental degradation may be just as important.

Along gradients of deposited sediment, reduced biomass and availability of invertebrate prey may contribute to ‘bottom-up’ processes affecting energy flow and species distributions in stream ecosystems (Angradi 1999, Osmundson et al. 2002, Suttle et al. 2004). By characterizing trophic structure along a sediment gradient using stable isotope metrics, we found evidence that changes in stream communities and ecosystem properties likely contributed to the reduced consumer $\delta^{13}\text{C}$ range and trophic niche-space ‘compression’. Changes to invertebrate communities included a decrease in the frequency of ‘grazers’ and ‘shredders’, and an increase in the relative frequency of ‘collectors’ and ‘deposit-feeders’. This functional shift in stream communities was coupled with a greater availability of fine benthic organic matter relative to other resources (Chl-a and CPOM), and a decrease in periphyton quality as measured by molar C:N ratios. The changes in periphyton quality may have been due to altered species composition

and greater incorporation of terrestrially-derived particulate matter with relatively higher C:N ratios. There was a strong correlation between the inorganic component of periphyton and sediment; also between the autotrophic index (ratio of AFDM to chl-a concentrations) and periphyton C:N (F. J. Burdon, *unpublished data*).

These changes in resources may have contributed to the greater proportion of detritus in the diets of invertebrate ‘grazers’ and ‘collectors’ along our sediment gradient, suggesting that niche homogeneity contributed to the narrowing consumer $\delta^{13}\text{C}$ range (Fig. 1c). Similar patterns have been observed in streams along a pH gradient; where greater acidity led to an increased reliance on detritus by invertebrate consumers (Layer et al. 2012). However, in our streams, the pattern is likely influenced by habitat degradation, mediated in part by flow, as cobble habitat is made unavailable by the deposition of fine inorganic sediment and associated periphyton communities degraded (Burdon et al. 2013). Concomitant with these changes, fine benthic organic matter increased in quantity, both in absolute terms and relative to other resources. Coupled with these changes in habitat and resources, ‘saltating’ sediment particles may exert additional stress on stream invertebrates (Culp et al. 1986). Thus, the sediment-induced degradation of habitat potentially caused a shift from a more complex food web partitioning the heterogeneous mixture of resources (periphyton/biofilms, detritus) to a food web dominated by generalist feeding on detritus (i.e., fine particulate organic matter); thus contributing to the narrowing consumer $\delta^{13}\text{C}$ range and the ‘compression’ of isotopic niche space. Similar to these results, Yule et al. (2010) found that increasing sedimentation in a tropical river led to simpler food webs, with fewer nodes and links, lower linkage density, and less complexity.

We postulated that four hypothetical consumer-resource interactions may have contributed to the extent of the niche breadth as measured by the consumer $\delta^{13}\text{C}$ range (Fig. 1).

Our results provide evidence suggesting all four of these processes may influence the consumer $\delta^{13}\text{C}$ range along the sediment gradient. Greater niche partitioning at low sediment levels leading to a wider consumer $\delta^{13}\text{C}$ range (Fig. 1a) appeared to be replaced by a mixture of processes reflecting the niche ‘generalists’, ‘homogeneity’ and ‘elimination’ hypotheses, which all predicted a narrowing of the consumer $\delta^{13}\text{C}$ range (Fig. 1b-d). Most invertebrate consumers are polyphagous (Allan and Castillo 2007), and results from isotopic mixing models in our study could be interpreted to show that the more generalist invertebrate taxa from the ‘collectors’ functional-feeding group exploited the abundant detrital resource (e.g., fine particulate organic matter) in streams with high levels of deposited sediment, thus supporting the niche ‘homogeneity’ hypothesis (Fig. 1c). Similar to our study, Yule et al. (2010) found that several taxa which were ‘grazers’ at sites unaffected by sediment became facultative ‘collectors’ at impacted sites. However, it was not clear whether this response was due to changes in relative availability of different resources with increased sedimentation, or resource scarcity forcing these invertebrates into more generalist-feeding modes.

Where a particular resource is ‘super-abundant’, it should be particularly attractive to all consumers by virtue of its abundance (Schoener 1974), thus reflecting the most likely scenario for the niche ‘homogeneity’ hypothesis (Fig 1c). However, optimal foraging theory predicts that food scarcity should lead to dietary convergence, because all species become generalists (Pyke et al. 1977), and consumers can demonstrate polyphagy and omnivory in streams where resource availability is low (Zah et al. 2001). These two examples reflects scenarios where the niche ‘generalists’ hypothesis may be prevalent. Reconciling these two theories may come from a better understanding of resource heterogeneity and habitat use (Schoener 1974, Pulliam 1986). Sediment not only potentially homogenizes resources, but also changes habitat (Waters 1995),

thus constraining the community available to feed on a given resource. In our study, analysis of isotopic mixing-model data using partial redundancy analysis indicated that sediment alone did not significantly explain the contribution of periphyton to primary consumers, meaning the sediment induced changes to community composition indirectly influenced resource use. These changes reflected increases in the relative frequency of invertebrate deposit-feeders with sedimentation, thus suggesting a shift to a community better adapted to consuming fine benthic organic matter (Fig 1c). Numerous other studies have documented the dominance of burrowing deposit-feeders such as oligochaetes, nematodes, and Chironomini (Chironomidae) in response to increased sediment deposition (Waters 1995), and these changes may reflect a greater abundance of fine benthic organic matter and associated heterotrophs (Nuttall and Bielby 1973, Winterbourn 2000). However, testing the relative contribution of these two processes (niche ‘generalists’ and ‘homogeneity’) to the increased trophic equivalence of primary consumers with sedimentation can only be resolved with experimentation, and it is likely that both apply to some extent in streams affected by sediment.

Although the relative contribution of niche ‘generalists’ and ‘homogeneity’ remain uncertain, we found abundances of more specialized invertebrate ‘grazers’ and ‘shredders’ decreased with sedimentation, thus supporting the niche ‘elimination’ hypothesis (Fig. 1d). Unequivocal evidence of this mechanism came with the loss of the rheophilic, algal-grazing caddisfly *Helicopsyche albescens* (Trichoptera: Helicopsychidae) as levels of deposited sediment increased (F. J. Burdon, *unpublished data*). Likewise supporting the niche ‘elimination’ hypothesis, Yule et al. (2010) reported the loss of ‘grazers’, ‘shredders’, and ‘filter-feeders’ with a large sediment disturbance in a tropical river. We found that abundance and diversity of benthic invertebrates was lowest in streams with more homogeneous substrate dominated by fine

sediment, a similar result to that reported elsewhere (Quinn and Hickey 1990). Larger substrate is typically more stable than smaller particles, thereby accumulating more periphyton and coarse organic matter (Quinn and Hickey 1990), and the greater availability of heterogeneous cobble habitat potentially helped to support the greater trophic diversity we observed in streams where levels of deposited sediment were low (F. J. Burdon, *unpublished data*). Substrate heterogeneity frequently has a strong positive correlation with diversity, a relationship often attributed to the "greater number of niches" in areas of more heterogeneous habitat (Beisel et al. 2000).

In our example, the trophic niche may converge with other dimensions of the fundamental niche (i.e. Hutchinson's n-dimensional hypervolume), if consumer-resource interactions are dependent upon environmental conditions. Because the trophic niche is a part of the fundamental niche (Leibold 1995), it should be expected that a combination of community and ecosystem changes associated with sedimentation may contribute to a 'compression' of isotopic niche space as trophic roles become influenced by other niche dimensions contributing to resource homogeneity. Alternatively, the increasing trophic equivalence of primary consumers suggests that neutral dynamics may govern community interactions where trophic niche differentiation is strongly reduced by environmental stress and loss of habitat (e.g., niche 'generalists'). Our findings further suggest that future research on explaining community structure and biodiversity should focus on synthesizing niche and neutral perspectives (Leibold and McPeck 2006). This is important, because although competitive exclusion can be a feature of lotic food webs (Kohler and Wiley 1997), it is generally considered that physical disturbance overrides the importance of biotic interactions in shaping benthic community composition (Peckarsky 1983, McAuliffe 1984, Poff and Ward 1989). However, recent studies have suggested that perturbations may strengthen biotic interactions (Thomson et al. 2002, Tylianakis

et al. 2007), and the greater trophic equivalence of stream consumers with increasing sedimentation suggests that competitive interactions may be amplified through reduced niche differentiation. These changes may have consequences for ecosystem functioning, if resource and habitat heterogeneity maximizes the effects of diversity through niche partitioning (Tylianakis et al. 2008). Moreover, sediment-induced changes to the energetic pathways of stream food webs may undermine ecosystem stability, reflecting predicted effects of structural asymmetry in trophic networks (Rooney et al. 2006).

Stable isotopes and stream biogeochemistry

A study investigating stream geomorphological influences on the variation of $\delta^{13}\text{C}$ among organic matter sources and consumers in a forested Piedmont river (South Carolina, USA) found that consumer $\delta^{13}\text{C}$ at rocky sites depended on algal carbon more than consumers at sandy sites (Walters et al. 2007). Paradoxically, however, they found that the consumer $\delta^{13}\text{C}$ range was greater at the sand sites; although their results may have been explained in part by a different selection criteria for SIA invertebrates and sampling a more pristine (i.e., forested) stream habitat. Moreover, the presence of wood as stable substrata for epixylic biofilms and xylophagous invertebrates at their sandy sites (47-74% of cover) was a notable habitat feature. In all our streams, large woody debris was essentially absent, which is typical of pastoral streams (Quinn 2000).

Biogeochemical processes at the microhabitat and ecosystem scale that may have affected the $\delta^{13}\text{C}$ of primary consumers and thus contributed to our results. Effects of carbon supply or photosynthetic effects on carbon isotope fractionation by benthic algae in streams may account for some of the changes in $\delta^{13}\text{C}$ between habitats (Finlay et al. 1999). In our study, deposited sediment was negatively correlated with mean flow velocity and variance. ‘Grazers’ in

fast-flowing habitats usually have more negative $\delta^{13}\text{C}$ values than other consumers in the same reach (Rounick et al. 1982). Finlay et al. (1999) found that primary consumer $\delta^{13}\text{C}$ varied according to river habitats and productivity, where increased water velocity lead to an increased supply of CO_2 relative to photosynthetic rates, thus negatively influencing ‘grazer’ $\delta^{13}\text{C}$. In contrast, when CO_2 concentrations are depleted in the boundary layer around benthic algae, effects of carbon limitation can result in enriched algal $\delta^{13}\text{C}$ (Hecky and Hesslein 1995). Similarly, warmer stream temperatures may contribute to lower dissolved CO_2 levels, thus influencing algal $\delta^{13}\text{C}$ (Finlay et al. 1999). Although altered flow regimes and stream productivity may have affected consumer $\delta^{13}\text{C}$ in our streams, there was no significant relationship between sediment and epilithic $\delta^{13}\text{C}$ (F. J. Burdon, *unpublished data*). It seems likely that changes to the invertebrate community and the increased abundance of fine particulate organic matter may have been more important in influencing the more homogenous $\delta^{13}\text{C}$ signature of consumers at sites with high levels of deposited sediment.

As in our study, Walters et al. (2007) were unable to record the $\delta^{13}\text{C}$ of epipelic biofilm (algal growing on the surface of sediment), but this omission may not have influenced our results, because epipelic biofilms are typically more heterotrophic than periphyton, and sand habitats can be important zones of bacterial processing of organic matter (Romani and Sabater 2001). Shifts towards heterotrophy have also been found in studies of stream ecosystem metabolism as sedimentation increases (Rier and King 1996, Atkinson et al. 2008). Thus, it seems likely that heterotrophy dominates in fine sediment-dominated benthic habitats, and may have contributed to the narrowing consumer $\delta^{13}\text{C}$ observed in our study.

Sediment influences on food-chain length

In contrast to the narrowing consumer $\delta^{13}\text{C}$ range, we observed no significant effects of sediment on food-chain length (FCL), as measured by maximum trophic position (MTP). Ecologists have long sought to identify the environmental determinants influencing FCL, and have focused on various theories including the effects of disturbance (dynamic constraints) and productivity (Pimm and Lawton 1977, Pimm 1982). In our study, there was little evidence of sediment disturbance affecting FCL, and community analyses indicated that sedimentation had weaker effects on stream fishes than benthic invertebrates. Stream systems are often highly disturbed (Resh et al. 1988), but sufficient refugia from physical disturbance may ensure localized extinctions of predators are rare events; thus dynamic constraints may operate only weakly, if at all (Thompson and Townsend 2005). These views were reiterated by Walters and Post (2008) who suggested that FCL may be an insensitive indicator of disturbance. In contrast, dissolved reactive phosphorus was strongly correlated with predator body size and food-chain length in our study. This lends support to the productivity hypothesis (Pimm 1982), because streams in New Zealand are typically phosphorus limited (McDowell et al. 2009). Overall, our results concur with a recent meta-analysis of food-web studies which supported the productivity hypothesis, but found equivocal evidence for dynamic constraints (Takimoto and Post 2012).

Despite this, lower fish production and reduced abundances have frequently been observed in streams affected by sedimentation (Waters 1995). A similar pattern may help explain the non-linear relationship between fish community trophic diversity and deposited sediment in our study, where a release from intra- and interspecific competition at high levels of sediment disturbance may have enabled resident fish to better partition available resources; as a corollary, fish found at silted sites may also have foraged over larger areas, and thus acquired more varied

isotopic signatures than other individuals at the same location. Despite the high levels of sediment pollution observed in their study, Yule et al. (2010) observed no effect on fish distribution and diets, which may have been influenced by prey subsidies. Spatial subsidies of terrestrial invertebrates, by mitigating the loss of preferred resources, may offset reduced benthic prey availability and help stabilize stream food webs, particularly where fish have generalist-feeding behaviors (Scrimgeour and Winterbourn 1989, Huxel and McCann 1998).

Concluding remarks

No single methodology, including stable isotopes analysis, can provide a complete description of food web structure and function (Layman et al. 2007). Some of the limitations of this approach have been alluded to, and importantly, total isotopic variation of a consumer is not only a function of trophic ecology, but of all factors that affect the assimilation of food items into tissue. These can include variability in fractionation where isotopic routing may differ among species (Deniro and Epstein 1981). Nevertheless, recent studies have highlighted the ability of stable isotopes to accurately match the isotopic niche with the trophic niche (Fink et al. 2012, Rodriguez and Herrera 2013). Moreover, traditional methods (e.g., gut contents analysis, GCA) possess considerable limitations. GCA is time-consuming, requires high levels of replication and taxonomic expertise, can overestimate certain dietary pathways, and is not time-integrative (Votier et al. 2003, Rybczynski et al. 2008). In contrast, one of the strengths of the community-wide isotopic approach is detecting overall patterns in food web structure that can then be further investigated using more traditional methods (Layman et al. 2007).

By using community-wide SIA, we have elucidated food-web responses that go further than traditional indices in highlighting the potential deleterious ecological consequences of stream sedimentation. Although there is strong evidence that habitat loss and degradation (e.g.,

lower substrate stability) contribute to much of the structural changes in invertebrate communities with sedimentation (Burdon et al. 2013), the increasing trophic equivalence of consumers suggests more complex effects of sediment on the functional properties of stream food webs. Our study provides strong evidence that degraded habitat and concomitant changes to stream communities (as measured by stable isotopes) leads to functionally less diverse food webs with a ‘compression’ of trophic niche-space.

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LITERATURE CITED

- Allan, D. J. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257-284.
- Allan, J. D., and M. M. Castillo. 2007. *Stream ecology: structure and function of running waters*. Springer, Dordrecht, The Netherlands.
- Anderson, C., and G. Cabana. 2009. Anthropogenic alterations of lotic food web structure: evidence from the use of nitrogen isotopes. *Oikos* 118:1929-1939.

- Angradi, T. R. 1999. Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society* 18:49-66.
- Atkinson, B. L., M. R. Grace, B. T. Hart, and K. Vanderkruk. 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Beisel, J. N., P. Usseglio-Polatera, and J. C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422:163-171.
- Burdon, F. J., A. R. McIntosh, and J. S. Harding. 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. *Ecological Applications* 23:1036–1047.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.
- Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences* 93:10844-10847.
- Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64:1345-1351.
- Deniro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica Et Cosmochimica Acta* 45:341-351.
- Fink, P., E. S. Reichwaldt, C. Harrod, and A. G. Rossberg. 2012. Determining trophic niche width: an experimental test of the stable isotope approach. *Oikos* 121:1985-1994.

- Finlay, J. C., M. E. Power, and G. Cabana. 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. *Limnology and Oceanography* 44:1198-1203.
- Haynes, R. J., and G. S. Francis. 1990. Effects of mixed cropping farming systems on changes in soil properties on the Canterbury Plains. *New Zealand Journal of Ecology* 14:73-82.
- Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* 14:631-653.
- Hoeinghaus, D. J., and S. C. Zeug. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. *Ecology* 89:2353-2357.
- Hutchinson, G. E. 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427.
- Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. *The American Naturalist* 152:460-469.
- Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, J. I. Jones, R. B. Lauridsen, M. E. Ledger, H. M. Lewis, J. M. Olesen, F. J. F. v. Veen, P. H. Warren, and G. Woodward. 2009. Ecological networks: beyond food webs. *Journal of Animal Ecology* 78:253-269.
- Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80:595-602.

- Jardine, T. D., R. A. Curry, K. S. Heard, and R. A. Cunjak. 2005. High fidelity: isotopic relationship between stream invertebrates and their gut contents. *Journal of the North American Benthological Society* 24:290-299.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055-1071.
- Kemp, P., D. Sear, A. Collins, P. Naden, and I. Jones. 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes* 25:1800-1821.
- Kohler, S. L., and M. J. Wiley. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78:2164-2176.
- Layer, K., A. G. Hildrew, and G. Woodward. 2012. Grazing and detritivory in 20 stream food webs across a broad pH gradient. *Oecologia* 171:459-471.
- Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, L. A. Yeager, D. M. Post, and S. Bearhop. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews* 87:545-562.
- Layman, C. A., D. A. Arrington, C. G. Montana, and D. M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42-48.
- Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371-1382.
- Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399-1410.

- MacLeod, C. J., and H. Moller. 2006. Intensification and diversification of New Zealand agriculture since 1960: An evaluation of current indicators of land use change. *Agriculture, Ecosystems & Environment* 115:201-218.
- McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65:894-908.
- McDowell, R. W., S. T. Larned, and D. J. Houlbrooke. 2009. Nitrogen and phosphorus in New Zealand streams and rivers: Control and impact of eutrophication and the influence of land management. *New Zealand Journal of Marine and Freshwater Research* 43:985-995.
- McHugh, P. A., A. R. McIntosh, and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters* 13:881-890.
- McIntosh, A. 2000. Aquatic predator-prey interactions. Pgs 125-156 *in* New Zealand stream invertebrates: ecology and implications for management. K. J. Collier and M. J. Winterbourn (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Newsome, S. D., C. Martinez del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5:429-436.
- Nuttall, P. M., and G. H. Bielby. 1973. The effect of china-clay wastes on stream invertebrates. *Environmental Pollution* 5:77-86.
- Osmundson, D. B., R. J. Ryel, V. L. Lamarra, and J. Pitlick. 2002. Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. *Ecological Applications* 12:1719-1739.
- Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672.

- Parnell, A. C., and A. L. Jackson. 2011. *siar: stable isotope analysis in R*. R Foundation for Statistical Computing, Vienna, Austria.
- Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of community structure. Pgs 303-324 *in* Dynamics of Lotic Ecosystems. T. D. Fontaine and S. M. Bartell (eds.). Ann Arbor Science Publishers Ann Arbor, MI, USA.
- Petchey, O. L., A. L. Downing, G. G. Mittelbach, L. Persson, C. F. Steiner, P. H. Warren, and G. Woodward. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467-478.
- Pimm, S. L. 1982. Food webs. Chapman and Hall, New York, USA.
- Pimm, S. L., and J. H. Lawton. 1977. Number of trophic levels in ecological communities. *Nature* 268:329-331.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature* 350:669-674.
- Poff, L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.
- Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution* 17:269-277
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703-718.
- Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179-189.

- Post, D. M., and G. Takimoto. 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116:775-782.
- Pulliam, H. R. 1986. Niche expansion and contraction in a variable environment. *American Zoologist* 26:71-79.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52:137-154.
- Quinn, J., and C. W. Hickey. 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24:411-427.
- Quinn, J. M. 2000. Effects of pastoral development. Pgs 208-229 *in* New Zealand stream invertebrates: ecology and implications for management. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- R Development Core Team, 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- Rier, S. T., and D. K. King. 1996. Effects of inorganic sedimentation and riparian clearing on benthic community metabolism in an agriculturally-disturbed stream. *Hydrobiologia* 339:111-121.
- Rodriguez, M. A., and L. G. Herrera. 2013. Isotopic niche mirrors trophic niche in a vertebrate island invader. *Oecologia* 171:537-544.

- Romani, A. M., and S. Sabater. 2001. Structure and activity of rock and sand biofilms in a Mediterranean stream. *Ecology* 82:3232-3245.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265-269.
- Rounick, J. S., M. J. Winterbourn, and G. L. Lyon. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. *Oikos* 39:191-198.
- Rybczynski, S. M., D. M. Walters, K. M. Fritz, and B. R. Johnson. 2008. Comparing trophic position of stream fishes using stable isotope and gut contents analyses. *Ecology of Freshwater Fish* 17:199-206.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Scrimgeour, G. J., and M. J. Winterbourn. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171:33-44.
- Stouffer, D. B. 2010. Scaling from individuals to networks in food webs. *Functional Ecology* 24:44-51.
- Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* 14:969-974.
- Takimoto, G. and D. Post. 2012. Environmental determinants of food-chain length: a meta-analysis. *Ecological Research* *in press* doi: 10.1007/s11284-012-0943-7.
- Thompson, R. M., J. A. Dunne, and G. Woodward. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology* 57:1329-1341.

- Thompson, R. M., and C. R. Townsend. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137-148.
- Thomson, J. R., P. S. Lake, and B. J. Downes. 2002. The effect of hydrological disturbance on the impact of a benthic invertebrate predator. *Ecology* 83:628-642.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.
- Townsend, C. R., R. M. Thompson, A. McIntosh, C. Kilroy, E. Edwards, and M. Scarsbrook. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters* 1:200-209.
- Tunney, T. D., K. S. McCann, N. P. Lester, and B. J. Shuter. 2012. Food web expansion and contraction in response to changing environmental conditions. *Nature Communications* 3:1105.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A.-M. Klein, N. Buchmann, J. Perner, and T. Tschardtke. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol* 6:e122.
- Tylianakis, J. M., T. Tschardtke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202-205.
- Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1142-1158.

- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Votier, S. C., S. Bearhop, A. MacCormick, N. Ratcliffe, and R. W. Furness. 2003. Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. *Polar Biology* 26:20-26.
- Walling, D. E. 1990. Linking the field to the river: Sediment delivery from agricultural land. Pgs 129-152 *in* Soil erosion on agricultural land. J. Boardman, I. D. L. Foster and J. A. Dearing (eds.). John Wiley, Chichester, UK.
- Walters, A. W., and D. M. Post. 2008. An experimental disturbance alters fish size structure but not food chain length in streams. *Ecology* 89:3261-3267.
- Walters, D. M., K. M. Fritz, and D. L. Phillips. 2007. Reach-scale geomorphology affects organic matter and consumer $\delta^{13}\text{C}$ in a forested Piedmont stream. *Freshwater Biology* 52:1105-1119.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.
- Waters, T. F. 1995. *Sediment in streams. sources, biological effects, and control*. American Fisheries Society, Bethesda, Maryland, USA.
- Winterbourn, M. J. 2000. Feeding ecology. Pgs 100-124 *in* New Zealand stream invertebrates: ecology and implications for management. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21:203-217.
- Woodward, G. 2009. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology* 54:2171-2187.

Yule, C. M., L. Boyero, and R. Marchant. 2010. Effects of sediment pollution on food webs in a tropical river (Borneo, Indonesia). *Marine and Freshwater Research* 61:204-213.

Zah, R., P. Burgherr, S. M. Bernasconi, and U. Uehlinger. 2001. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* 46:871-882.

SUPPLEMENTAL MATERIAL

Appendix A

Detailed descriptions of data collection methods.

Appendix B

Primary consumers used to calculate $\delta^{15}\text{N}$ baselines.

Appendix C

Detailed descriptions of statistical methods and regression models tested.

Appendix D

Additional results from analyzes of community data.

CHAPTER 4: PREAMBLE

Chapter 4 follows on from the previous chapters by considering the question: Does ecosystem function change in response to sedimentation? Using food webs as a systems approach representing patterns of biodiversity and energy flow helps to link factors affecting communities to those influencing ecosystem processes (Thompson et al. 2012). However, there are limits to what this approach can tell us, and in Chapter 3 it is not clear whether sedimentation weakens consumption of coarse detrital material, despite the abundances of specialized ‘shredding’ invertebrates appearing to decrease with increasing sediment. My inability to discern the relative contribution of different detrital resources to invertebrate consumers using isotopic mixing-model analyses was due to inconsistent isotopic fractionation of fine benthic organic matter. However, decreased invertebrate taxa richness, increasing trophic equivalence of primary consumers, and greater resource homogeneity along the sediment gradient in Chapter 3 indicated that ecosystem function (i.e., detrital processing) could be impaired. One reason this might happen is because greater resource heterogeneity is expected to increase niche partitioning, thus enhancing the relationship between biodiversity and ecosystem function (Tylianakis et al. 2008). Moreover, despite the ubiquity of sediment impacts in streams affected by human land uses and the importance of the detrital pathway to stream ecosystems, sediment influences on litter decomposition remain poorly understood. Thus, using detrital processing as a model ecosystem function in Chapter 4, I consider the potential influences of sediment at the ecosystem scale. The most powerful methodology to test mechanistic process is often through experimentation. Thus, in this chapter, I performed *in situ* litter breakdown assays in nine streams along a sediment gradient with three different treatments. To further elucidate these results and reduce potential “in the field” confounding factors, I also conducted controlled experiments using laboratory

mesocosm experiments to test the effects of sedimentation on consumer-resource interactions using leaf litter and detritivorous caddisflies.

LITERATURE CITED

- Thompson, R., U. Brose, J. Dunne, R. Hall, S. Hladyz, R. Kitching, N. Martinez, H. Rantala, T. Romanuk, and D. Stouffer. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution* 27:689-697.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A.-M. Klein, N. Buchmann, J. Perner, and T. Tscharnkte. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol* 6:e122.

CHAPTER 4

SEDIMENTATION LEADS TO CASCADING EFFECTS ON BIODIVERSITY, CONSUMER-RESOURCE INTERACTIONS, AND ECOSYSTEM FUNCTION IN AGRICULTURAL STREAMS



Leaf-packs in a stream affected by sedimentation near MacLeans Island, Canterbury Plains.

Abstract. Agricultural intensification can exert pressure on stream ecosystems through the removal of riparian vegetation and by increasing inputs of diffuse pollutants (e.g., fine inorganic sediment). Such changes to environmental context can strongly influence stream communities and their interactions, whilst potentially also affecting aquatic-terrestrial linkages and associated ecosystem functions. Revegetation of riparian zones may help to mitigate agricultural impacts, but sediment pollution can have continuing legacy effects. These can reduce the availability of terrestrial detritus through burial and alter invertebrate community diversity and composition, thus potentially leading to impaired detrital processing. To investigate this issue, we surveyed litter breakdown in nine agricultural streams along gradients of sediment and dissolved nutrients, and examined potential mechanisms of sediment effects through laboratory microcosm experiments. Detrital processing rates were slower with increased levels of deposited sediment. Although sediment only had a weak negative effect on leaf microbial activity, invertebrate communities changed significantly with increasing sedimentation. As a result, reduced abundances and richness of detritivorous caddisflies strongly contributed to decreased ecosystem function. In experimental stream mesocosms, the burial of leaves by sediment made this resource less available to the detritivorous caddisflies *Olinga feredayi* (Conoesucidae) and *Triplectides obsoletus* (Leptoceridae), thus reducing rates of litter breakdown and larval growth. Overall, our results indicate sedimentation directly and indirectly affects detrital processing through changes to resource availability and invertebrate community composition. Thus, environmental context not only potentially controls the magnitude of cross-ecosystem subsidies, but also the availability of resources to recipient food webs. Our findings suggest that efforts to rehabilitate streams should focus on improving habitat conditions affecting both donor and recipient communities so as to help restore aquatic-terrestrial linkages and associated ecosystem functions.

Keywords: agricultural land uses; aquatic-terrestrial linkages; detrital processing; global change; resource subsidies; riparian management; stream health; stream invertebrate communities

INTRODUCTION

The world's ecosystems are facing unprecedented rates of change, driven in part by extensive habitat loss and degradation associated with intensive human land-uses (Tylianakis et al. 2008a). This can alter species distributions, potentially impacting biotic interactions with pervasive consequences for ecosystem functioning and food-web stability (Tylianakis et al. 2007). Although freshwaters account for less than 1% of the earth's surface, they provide habitat for ~10% of global biodiversity, meaning human impacts affecting freshwaters may disproportionately contribute to species extinctions and loss of biodiversity (Strayer and Dudgeon 2010). Agricultural land uses dominate human land uses, and affect streams through multiple pathways including the degradation of riparian and in-stream habitat, leading to deleterious changes in stream communities (Allan 2004). In particular, the loss of riparian vegetation due to agricultural practices can reduce inputs of detritus (Reid et al. 2008) and terrestrially-derived prey (Edwards and Huryn 1996), whilst increasing diffuse pollution including fine inorganic sediment (Jones et al. 1999). Such changes to environmental context are likely to strongly influence biological communities and their interactions, especially by affecting cross-ecosystem linkages and associated ecosystem functions like detrital processing.

Intensification of agricultural land uses may profoundly impact metabolic processes, energy flow, and food-web stability of freshwater ecosystems by altering inputs of terrestrial subsidies (Kominoski and Rosemond 2011). The importance of terrestrially-derived detrital subsidies to streams is well known (Fisher and Likens 1973), but cross-ecosystem linkages have

only recently been incorporated into theory connecting landscapes and food webs (Polis et al. 1997). Resource gradients in donor habitats can affect the magnitude of subsidies entering adjacent habitats (Polis and Hurd 1996), but how environmental context modulates effects on recipient food webs is still poorly understood (Marczak et al. 2007). Recipient habitat productivity, boundary properties, and habitat size all potentially influence the importance of resource subsidies (Marczak et al. 2007, Polis and Hurd 1996), but recent evidence suggests recipient community composition can affect the uptake of donor resources, thus adding to a growing consensus that species identities can be an important determinant of ecosystem functioning (Romero and Srivastava 2010). However, few studies have explicitly linked the effects of natural and anthropogenic disturbance on communities to resource subsidy influences (Greenwood and McIntosh 2008, Paetzold et al. 2011). Moreover, the potentially important impacts of sedimentation on aquatic-terrestrial linkages have seldom been considered, despite the obvious implications for freshwater ecosystems (*cf.* Laeser et al. 2005).

Degradation caused by inputs of sediment to streams and rivers is a widespread and pervasive problem often associated with agriculture (Walling 1990, Wood and Armitage 1999). Sedimentation can adversely affect benthic algal communities, leading to reduced productivity and heterotrophic dominance (Rier and King 1996). Numerous studies have shown that sediment strongly influences stream invertebrate communities, leading to reduced diversity, altered community composition, and threshold responses (Jones et al. 2012, Burdon et al. 2013). These influences may also lead to reduced abundances and richness of ‘shredding’ detritivores, thus potentially contributing to slower litter breakdown rates (Sponseller and Benfield 2001, Yule et al. 2010). Moreover, the burial of organic matter by fine sediment may impair detrital breakdown by creating hypoxic conditions, reducing detrital surface area for microbial colonization, and

decreasing physical abrasion (Pascoal et al. 2005), whilst potentially also changing leaf chemistry and palatability (Herbst 1980) and restricting accessibility of resources to detritivorous invertebrates (Navel et al. 2010).

Despite these possible effects, there are still gaps in our knowledge regarding the consequences of diffuse pollutants from agricultural land uses on stream detrital processing (Niyogi et al. 2003). Understanding the effects of sedimentation on stream food webs and key ecosystem functions such as decomposition is critically important, because although the planting of vegetated buffer strips can help mitigate the effects of agricultural land uses (Lake et al. 2007), temporal and spatial legacy effects of sediment may diminish the benefits of riparian rehabilitation (Harding et al. 1998, Allan 2004, Greenwood et al. 2012). Legacy effects, including that of sediment, may help to explain why the ‘field of dreams’ model of stream restoration has seldom delivered the benefits desired (Sudduth et al. 2011).

We investigated whether sedimentation in agricultural streams was negatively associated with detrital processing and invertebrate diversity and community composition, including abundances of detritivorous caddisflies. It was hypothesized that deposited fine inorganic sediment (<2 mm) would adversely impact stream detrital breakdown, with impairment driven principally by altered resource availability (burial leading to reduced abrasion, litter quality, and accessibility) and decreases in detritivores. To better elucidate mechanisms affecting litter breakdown rates and invertebrates, we used laboratory experiments to investigate how burial of detrital resources by sediment affected litter consumption, growth, and mortality rates of detritivorous caddisflies.

METHODS

Study sites

We studied streams on the Canterbury Plains, located on the eastern side of New Zealand's South Island. European settlement has seen arable production (pasture, livestock, and cropping) become the dominant land use in this region (Haynes and Francis 1990), with increasing intensification in the past three decades (MacLeod and Moller 2006). As a consequence, the dominant vegetation has changed from a mosaic of forest, shrublands, and wetlands prior to human settlement (Wardle 1991), to pasture (introduced grasses and *Trifolium* spp.) and monocultures of crops, interspersed with windbreaks and hedgerows of introduced conifers (*Cupressus* and *Pinus* spp.), poplars (*Populus* spp.), and willows (*Salix* spp.). This vegetation is also the principal form of riparian plantings, and windbreaks and hedgerows can often be found alongside streams and water races.

Nine first to third order streams with perennial flow were selected to fit nutrient and substrate composition criteria, with three streams selected in each of three nutrient and three sediment categories, leading to a three by three orthogonal design. These categories were used only for site selection; sediment and nutrient have been treated as continuous variables for analyses. Nutrient status was judged as 'low' ($<100 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$), 'medium' ($100 - 162 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$), and 'high' ($>162 \mu\text{S}_{25^\circ\text{C}}/\text{cm}$) based on spot measures of specific conductivity (YSI 63, YSI Incorporated, Yellow Springs, OH, USA). Conductivity has been strongly correlated with total nitrate concentrations in these streams (Greenwood et al. 2012). Three levels of nutrients (e.g., nitrate concentrations) were used to help reduce the potentially confounding effects of enrichment on stream communities and decomposition (Hladysz et al. 2010). For deposited sediment, sites were categorized as 'low' ($<15\%$), 'medium' ($15\% - 50\%$) and 'high' ($>50\%$),

according to the proportion of fine inorganic sediment (< 2mm particle size) covering the streambed in a 30 m reach. Bank-side visual estimates of sediment cover are strongly correlated to physical sediment measurements (Clapcott et al. 2011). All reaches were located on separate tributaries, comprised of run-riffle sequences (pool habitat <2.5% of total channel area), and had less than 40% submerged macrophyte cover.

Survey data collection

Spot measurements of pH, specific conductivity (YSI 63), and dissolved oxygen (YSI 550A) were made monthly from December 2010 to April 2011. Water samples (100 ml) were collected for nutrient analysis, filtered (LabServ[®], Thermo Fisher Scientific New Zealand Ltd., North Shore City, NZ, GF/F, 25 mm diameter) into opaque, acid-washed bottles, placed on ice, and frozen upon return to the laboratory. Samples were tested for nitrate (nitrate and nitrite nitrogen; mg/L) and DRP (dissolved reactive phosphorus; µg/L) using a SYSTEAs Easychem discrete colorimetric auto-analyzer (SYSTEAs S.p.A., Anagni, Italy). Ammonia was not measured as concentrations are very low in these streams (Greenwood et al. 2012). Nitrate and DRP were analyzed using the cadmium reduction and the molybdate reduction methods respectively (APHA 1995). A further 1 L water sample was collected mid-column from the thalweg for estimation of total suspended solids (mg/L). These water samples were filtered through a pre-ashed, pre-weighed glass fibre filter (LabServ[®] GF/F, 45 mm Ø) before drying (50° C, 24 hours), weighing, ashing (550° C, 6 hours) and reweighing. Stream sediment cover was visually estimated monthly (December 2010 to April 2011), and mean values correlated with previously recorded physical measures of fine inorganic sediment at the same sites (Burdon et al. 2013). In each reach, stream temperature was monitored continuously throughout the study

period with data loggers (HOBO Pendant[®] Temperature/Light Data Logger, Onset Computer Corporation, Bourne, MA, USA).

To measure decomposition rates in the streams, senescent red beech (*Nothofagus fusca*) leaves, collected from Arthur's Pass National Park, Central South Island, NZ, were air-dried at room temperature (~20° C) for ~14 months before being weighed into 8 g (dry-mass) leaf packs using coarse nylon bags (1 cm-mesh). Red beech leaves were selected for their moderate breakdown rates (Parkyn and Winterbourn 1997). Ten leaf packs were transported to field sites, submerged in stream water for ten minutes, and then returned to the laboratory, where they were sorted, dried (50° C, 24 hours), weighed, ashed (550° C, 6 hours), and reweighed. This procedure was used to estimate mass loss during transport, and to provide an initial starting biomass value for leaf packs (6.45 ± 0.02 , AFDM g ± 1 SE). Thirty-six leaf packs were then deployed in each of the nine streams; three replicates of four packs were allocated to each of the three following treatments: exposed, protected, and buried. The 'exposed' treatment allowed leaf packs to experience the full range of physical conditions including abrasion mediated by flow, whereas the 'protected' treatment leaf packs were placed in perforated PVC tubes, and anchored to the streambed. In the third treatment, leaf packs were buried to a depth of 10 cm in the dominant substrate (e.g., pebbles, gravel, or sand); these were placed downstream of the 'exposed' and 'protected' treatments. Flow velocities (Marsh-McBirney Flo-Mate Model 2000, Hach, Loveland CO, USA) at groups of leaf packs ($n = 9$) were recorded in January 2011. Leaf packs were collected after 7, 21, and 72 days (January – April 2011). A kicknet (250 μ m-mesh) was placed downstream of the leaf packs to help reduce the loss of sediment and invertebrates during collection. Bagged samples were placed in ice before being frozen upon return to the laboratory.

After 72 days (April 2011), three leaves were removed from each leaf pack for measurement of microbial respiration following the methods of Niyogi et al. (2003). The leaves were rinsed to remove sediment and then incubated at 16° C for six hours in closed vials containing stream water along with two blanks per site (stream water only). Following incubation, dissolved oxygen concentrations (mg/L; YSI 550A) were measured in each vial. The difference between the average concentration in blanks and those with leaves was used to calculate oxygen consumption. Leaves were then dried, weighed, and ashed to provide an estimate of biomass (AFDM), which was used to calculate the net rate of oxygen consumption by leaves ($\text{O}_2 \text{ mg L}^{-1} \text{ hour}^{-1} \text{ AFDM g}^{-1}$).

Intact leaves were removed from thawed leaf packs using forceps, and the remaining material was elutriated to separate organic and inorganic matter. Organic fractions were sieved (<2 mm), dried, weighed, and ashed to obtain estimates of biomass (AFDM); inorganic sediment (<2 mm) was weighed and dried. To calculate litter breakdown rates per day (k) and per degree-day (k_{dd}), we regressed the natural log (ln) of % AFDM remaining according to days of exposure (or cumulative temperature as degree-days) using the AFDM of the ‘handling loss’ leaf packs as 100% remaining for Day 0 (Benfield 2007). Samples were passed through a 250- μm sieve and all invertebrates present removed and identified to the lowest practicable level (e.g., usually genus) using appropriate identification guides (e.g., Winterbourn et al. 2006). The detritivorous caddisflies (Trichoptera) that may have contributed to litter breakdown are listed in Appendix A. Invertebrates from one leaf pack per treatment for each site were recorded for the Day 21 collection; all three replicate leaf packs per treatment were processed for Days 7 and 72.

Experimental design

Red beech (*Nothofagus fusca*) leaves were conditioned in a stream of low-nutrient status (Table 1; Waihikuawa Stream; WS henceforth) on the Canterbury Plains for six weeks (February-April 2011) prior to the commencement of laboratory experiments. Two complementary microcosm experiments using 48 containers (2 L) were conducted in a temperature-controlled room (16° C). During the experiments, ammonia levels were assessed (Ammonia NH₃/NH₄⁺ Test Kit, API Aquarium Pharmaceuticals, Chalfont, PA, USA), and a third of the WS stream water in each container changed weekly over the duration of both experiments. Containers were aerated continuously to create a gentle current and maintain dissolved oxygen levels at approximately 9 mg/L. A shelving unit with four levels accommodated the mesocosms, and the experiments were blocked according to shelving level.

The first experiment (Experiment 1) tested the effect of sediment burial on litter breakdown in the presence of an obligate shredder. Experiment 1 had two sediment (present and absent) and two caddisfly treatments (present and absent) leading to a randomized block two-way factorial design. Each combination of treatments was replicated in twelve containers. We first introduced 12 g of blotted, pre-conditioned leaf litter to each mesocosm (1.13 ± 0.05 AFDM, $g \pm 1$ SE, $n = 12$), and then added 165 g of dried river sand (Cyclone Sand, Gardenmakers, Christchurch, NZ) to sediment treatments (i.e., 0.73 g/cm^2). Sand was washed through a 45 μm -mesh sieve to remove residual clay particles. The sand grain size distribution matched measured fractions of fine sediment (2, 1, 0.5, 0.25, 0.125, and 0.045 mm) collected from study streams. Mid to late-instar larvae of an obligate ‘shredding’ caddisfly *Triplectides obsoletus* (Trichoptera: Leptoceridae) collected from the WS stream were the detritivorous consumers used in Experiment 1. Four individuals from three size classes (small, medium, and large; determined

from case length, likely representing instars 3, 4, and 5) at a ratio of 1:2:1 were added to each treatment mesocosm. Three mesocosms of each treatment were randomly allocated to each shelf.

The second experiment (Experiment 2) compared the effect of litter burial by sediment on two detritivorous caddisflies. Experiment 2 used a randomized-block replicated experimental-regression design with six treatment levels of sediment ranging from 0 to 1 g/cm². Each treatment was replicated four times, with each replicate randomly allocated to an experimental block (i.e., shelf). We introduced 25 g of blotted, pre-conditioned leaf litter (3.47 ± 0.05 AFDM g; $n = 10$) to each mesocosm, and then added washed Cyclone sand in increments of 0, 14, 28, 56, 113, and 225 g respectively, leading to treatment levels of 0, 0.06, 0.13, 0.25, 0.50, and 1 g/cm². These treatment levels were comparable to the range of sediment levels observed in the field. The detritivorous consumers used in Experiment 2 were mid to late-instar larvae of the caddisfly *Triplectides obsoletus*, collected from WS, and *Olinga feredayi* (Trichoptera: Conoesucidae), collected from the Okuti Stream, Banks Peninsula. We added ten individuals of a caddisfly taxon belonging to three size classes (small, medium, and large; determined from case length) to each treatment mesocosm at a ratio of 3:4:3.

Both experiments were run for 27 days, at which time intact leaves were removed from each mesocosm before separating the remaining organic material using nested Endecott sieves (2, 1, 0.5, 0.25, and 0.045 mm). Organic matter fractions were dried, weighed, and ashed to obtain estimates of biomass (g AFDM) and to calculate breakdown rates (mg/day). Leaf microbial respiration from each mesocosm was calculated by incubating three randomly-selected leaves as described earlier.

In Experiment 2, growth rate estimates of *Olinga* larvae were obtained by measuring the amount of case material secreted during the experiment. This caddisfly has a case made from

hard, secreted protein and newly laid down material could be readily distinguished (and measured with an eyepiece micrometer inserted in a stereo microscope at x 10 magnification) from that present at the start of the experiment. To calculate the percentage of new case material, total case length of *Olinga* individuals was also measured. In both experiments, individual larvae (removed from their cases) and the moulted sclerites (e.g., head capsule and metanotum; termed hereafter ‘exuviae’) recovered from mesocosms were dried, weighed, ashed, and reweighed. According to metabolic theory, feeding rates depend on body size (Brown et al. 2007). Thus, ‘metabolic body mass’ was calculated by raising invertebrate biomass to the power of $\frac{3}{4}$ (Kleiber 1947).

Data analysis

Data were transformed to meet assumptions of analyses including normality, homogeneity, and linearity. The mean proportion of fine inorganic sediment (<2 mm) covering the streambed was logit-transformed following Warton and Hui (2010), and to aide interpretation of results, a constant (2) was added to each score to transform negative values to positive integers. For the analysis of data from laboratory Experiment 2, sediment (g/cm^2) was square-root transformed. Invertebrate community density data (individuals/g AFDM) from leaf pack treatments were pooled according to sampling date and stream, averaged (e.g., $n = 3$), and square-root transformed before community composition using Bray-Curtis similarity was analyzed by means of non-metric multi-dimensional scaling (NMDS) in Primer (Version 6.1.12, Primer-E Ltd., Devon, UK). An additional NMDS was conducted on invertebrate densities for all leaf packs collected on Day 72. To aide interpretation of results, a constant (2) was added to each NMDS score to transform negative values to positive integers. Invertebrate taxa richness indices were rarefied using the “vegan” package in R (Oksanen et al. 2010); rarefied richness was

calculated for 100 individuals. Where appropriate, data were log-transformed ($\log_{10}+1$) to help meet statistical assumptions. Pearson's product moment correlations of physicochemical variables were conducted in R (R Development Core Team 2010).

We analyzed the majority of data from the litter breakdown assay and laboratory Experiment 2 using linear mixed-effects models (LMEM) with the packages "nlme" (Pinheiro et al. 2009) and "lme4" (Bates et al. 2011) in R. Normality and homogeneity were checked using visual inspections of residuals plotted against fitted values. To assess the validity of the mixed-effects analyses, likelihood ratio tests were used to compare the models with fixed effects to the null models with only the random effects (Zuur et al. 2009). Results were rejected in which the model including fixed effects did not differ significantly from the null model. Maximum likelihood ratio testing was also used to identify where non-significant interaction terms could be eliminated (Zuur et al. 2009). We used the restricted maximum likelihood method (REML) to estimate error terms for these LMEM, and unless stated otherwise, the 'varIdent' command was used to accommodate different variances for streams (Zuur et al. 2009).

The effects of leaf pack treatments (exposed, protected, and buried) and deposited sediment cover on litter breakdown (k_{dd}), microbial activity ($\text{O}_2 \text{ mg L}^{-1} \text{ hour}^{-1} \text{ AFDM g}^{-1} \text{ leaf}$), and the sediment ratio (inorganics < 2mm/AFDM litter at Day 72) were tested using a random intercepts model, thus treating streams as experimental 'blocks'. For community composition and rarefied taxa richness, a random intercepts model was used including both stream and time as random effects. The initial model for the response of detritivorous caddisfly densities (from individual leafpacks) failed to meet assumptions of normality and homogeneity, so in addition to stream as a random effect, different variances per stratum were allowed for the interaction between treatment and time using the 'varIdent' command (Zuur et al. 2009). A random

intercepts model to account for stream effects was used to test the influence of the sediment ratio and leaf pack treatments on microbial activity and the invertebrate response variables. The initial sediment ratio model for the response of litter breakdown (k_{dd}) failed to meet statistical assumptions, so we tested for influences using a generalized linear mixed-effects model (GLMM) with the ‘glmmPQL’ function in the R package “MASS” (Ripley et al. 2013). This model was fit with a quasibinomial distribution and streams as a random effect. Finally, we tested the influence of detritivorous caddisflies densities and microbial activity separately on litter breakdown using a random intercepts model to account for stream effects.

A randomized-block ANOVA was used to analyze the data from Experiment 1 with Tukey’s HSD post-hoc tests conducted in R. The effects of sediment and detritivore treatments (present or absent) were tested on the response of CPOM mass loss (mg/day), CPOM mass loss per total detritivore metabolic biomass (mg AFDM), microbial activity, total and individual detritivore biomass, growth ($\text{mg exuviae day}^{-1} \text{ mg total metabolic body mass}^{-1}$) and % mortality. The same response variables from Experiment 2 (also including *Olinga* % case growth) were analyzed using a random intercepts LMEM, thus accounting for the effect of randomized experimental ‘blocks’ on the response variables. The “lme4” package was used to analyze this data and we have presented Markov chain Monte Carlo (MCMC)-estimated p -values considered significant at $\alpha = 0.05$. These were generated using the ‘pvals.fnc’ function in the R package “languageR” (Baayen 2012). The % caddisfly mortality data did not meet the assumptions of homogeneity and normality, thus a GLMM with a binomial distribution was used.

RESULTS

Stream physico-chemical variables

A wide range of deposited sediment and dissolved nitrate concentrations were observed in the field survey (Table 1), but these two variables were not correlated (Pearson's product-moment correlation, $r = 0.20$, $p = 0.61$). The % sediment cover in the present study was strongly correlated with previously recorded measures of sediment from the same sites. These measures were reduced using principal components analysis to a sediment index which correlated strongly with % sediment cover in this study ($r = 0.96$, $p < 0.001$). The sediment index included suspendable inorganic sediment (g/m^2 ; $r = 0.69$, $p < 0.05$) and sediment depth (mm, $r = 0.90$, $p < 0.01$) which were both correlated with % sediment cover in the present study. For further details of these sediment metrics see Burdon et al. (2013). In the present study, the ratio of inorganic sediment ($< 2\text{mm}$) to remaining litter in leaf packs on day 72 (sediment ratio henceforth) was also significantly correlated with % sediment cover ($r = 0.76$, $p < 0.05$). Deposited sediment cover was negatively correlated with mean flow velocity ($r = -0.85$, $p < 0.01$), but there were no significant correlations with any other measured variables.

Leaf pack breakdown, microbial activity, and invertebrates

The leaf pack treatments (exposed, protected, and buried) and sediment predictor variables were significantly associated with litter breakdown and leaf pack invertebrates (Figs. 1 and 2; Appendix B). In all treatments, litter breakdown (k_{dd}) was significantly slower with increased deposited sediment cover (Fig. 1a; Appendix B Table 1). Litter breakdown rates were significantly slower in the buried treatment (LMEM, $t_{2,67} = -3.39$, $p < 0.01$) and the rate of decline in k_{dd} along the sediment gradient was slower in the protected treatment (LMEM, $t_{2,67} = 2.53$, $p < 0.05$, Fig 1a). In contrast, litter breakdown only significantly slowed with an increasing

TABLE 1. Mean physico-chemical variables recorded monthly (December 2010 – April 2011) from nine streams located on the Canterbury Plains, South Island, New Zealand. pH data was recorded, and typically approached circum-neutrality (mean range 7.1-7.6). The sediment ratio refers to the amount of inorganic sediment <2 mm (g) relative to the total leaf litter remaining (AFDM g) at Day 72. SIS, suspended inorganic sediment; DRP, dissolve reactive phosphorus; DO, dissolved oxygen.

Sediment	Stream	Location		% sediment cover	Physical				Chemical				
		Latitude	Longitude		Sediment ratio	SIS (mg/L)	Flow (m/s)	Temperature (°C)	Nitrate (mg/L)	DRP (µg/L)	Conductivity (µS _{25°C} /cm)	DO (mg/L)	% DO
Low	Cridges	-43.469	172.549	9	1.6	1.3	0.23	15.2	0.13	24.9	75	9.8	117
	Southbrook	-43.323	172.592	4	0.9	0.9	0.20	14.1	1.26	14.4	147	9.2	91
	Cust	-43.346	172.563	2	2.3	1.8	0.30	15.4	4.83	15.0	197	10.2	102
Med	Waihikuawa	-43.435	172.585	22	7.8	0.7	0.25	13.2	0.13	11.0	73	7.4	71
	Saltwater	-43.257	172.669	20	5.7	2.6	0.25	13.6	0.23	25.6	115	9.5	92
	Flaxton	-43.340	172.602	44	8.5	2.9	0.22	16.2	1.87	14.0	163	10.2	108
High	Shipleys	-43.459	172.566	76	4.0	1.1	0.14	15.1	0.21	14.0	78	8.4	87
	Springs	-43.655	172.482	100	10.0	2.1	0.06	13.5	1.91	19.0	162	7.0	68
	Leeston	-43.757	172.289	90	12.1	1.6	0.06	15.2	9.97	11.0	320	10.9	85

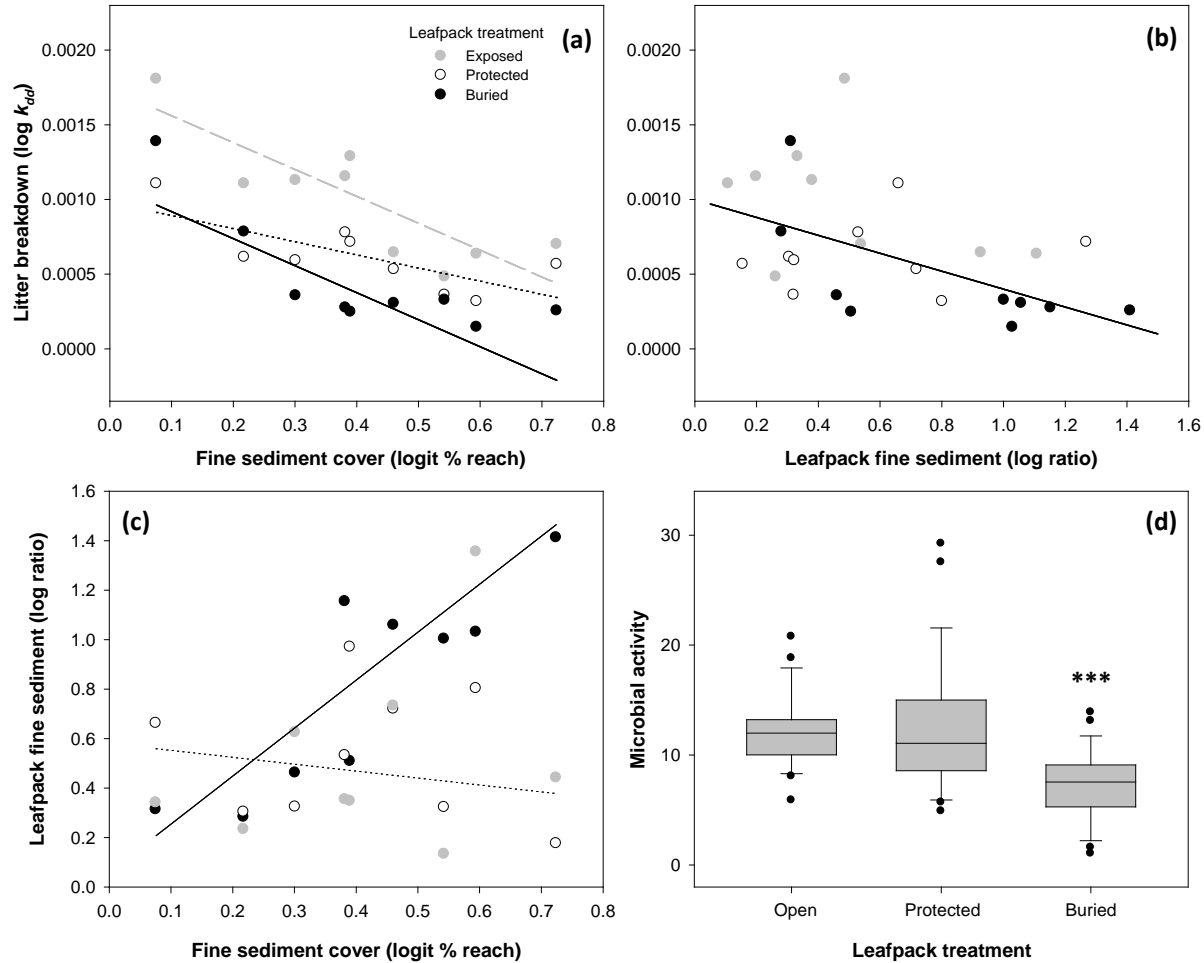


FIG. 1. Results from a field experiment on the Canterbury Plains, South Island, NZ, testing the influence of leaf pack treatments (exposed, protected, and closed) and deposited sediment on litter breakdown (k_{dd} , g AFDM/degree day) and microbial activity (O_2 mg L⁻¹ hr⁻¹ g⁻¹ AFDM leaf) along a sedimentation gradient in nine agricultural streams sampled during the austral summer of 2010/2011. (a) Litter breakdown rates from leaf pack treatments along a gradient of deposited sediment (logit sediment % cover). (b) The relationship of litter breakdown with the ratio of sediment (inorganic particles < 2mm) to remaining leaf litter in leaf pack treatments at Day 72. (c) The relationship of the sediment ratio and % sediment cover in leaf pack treatments. (d) Box-plots of un-transformed leaf microbial activity data recorded from different leaf pack treatments at Day 72. Unless stated otherwise, mean log-transformed ($\log_{10}+1$) data is presented. Where appropriate, regression lines indicate significant influences ($\alpha = 0.05$) of sediment and leaf pack treatments. Grey-dashed line, exposed treatments; black-dotted, protected; black-solid, buried. See text and Appendix B (Table 1) for statistical results. *** $p < 0.001$.

sediment ratio in the buried treatment (GLMM, $t_{2,67} = -3.17$, $p < 0.01$, Fig. 1b). The sediment ratio in buried leaf packs increased significantly with deposited sediment cover (LMEM, $t_{2,63} = 5.20$, $p < 0.001$, Fig. 1c). Microbial activity was significantly lower in the buried treatments across all streams (ANOVA, $F_{2,67} = 25.8$, $p < 0.001$, Tukey's HSD, $p < 0.001$, Fig. 1d), but was not significantly influenced by deposited sediment (Appendix B Table 1).

Over the three sampling periods (Days 7, 21, and 72), deposited sediment cover was associated with changes in invertebrate community composition (NMDS Axis 1 scores) in all three treatments (Fig. 2a, Appendix B Table 2). Community composition was significantly different in buried treatments compared to the exposed treatments (LMEM, $t_{2,70} = -3.90$, $p < 0.001$). In contrast, the sediment ratio in leaf packs on Day 72 was only negatively associated with community composition in the buried treatments from this collection period (LMEM, $t_{2,62} = -2.52$, $p < 0.001$, Fig. 2b). Changes to community composition over the three sampling periods (Days 7, 21, and 72) partly reflected the decrease in abundances of detritivorous caddisflies in all treatments with increasing sediment cover (Appendix B Table 3, Fig. 2c). We found significantly less detritivorous caddisflies in the protected leaf packs than the buried and exposed treatments (LMEM, $t_{2,62} = -6.44$, $p < 0.001$). However, on Day 72, abundances of these detritivores in leaf packs only significantly declined with an increasing sediment ratio in the buried treatment (LMEM, $t_{2,62} = -3.02$, $p < 0.05$, Fig. 2d). The rarefied richness of detritivorous caddisflies in leaf packs declined significantly with increasing sediment cover in all treatments (Appendix B Table 3, Fig. 2e). We found a significant positive association of abundances of these detritivores with litter breakdown in all three treatments (Appendix B Table 4, Fig. 2f). In contrast, microbial activity had no statistically significant influence on litter breakdown.

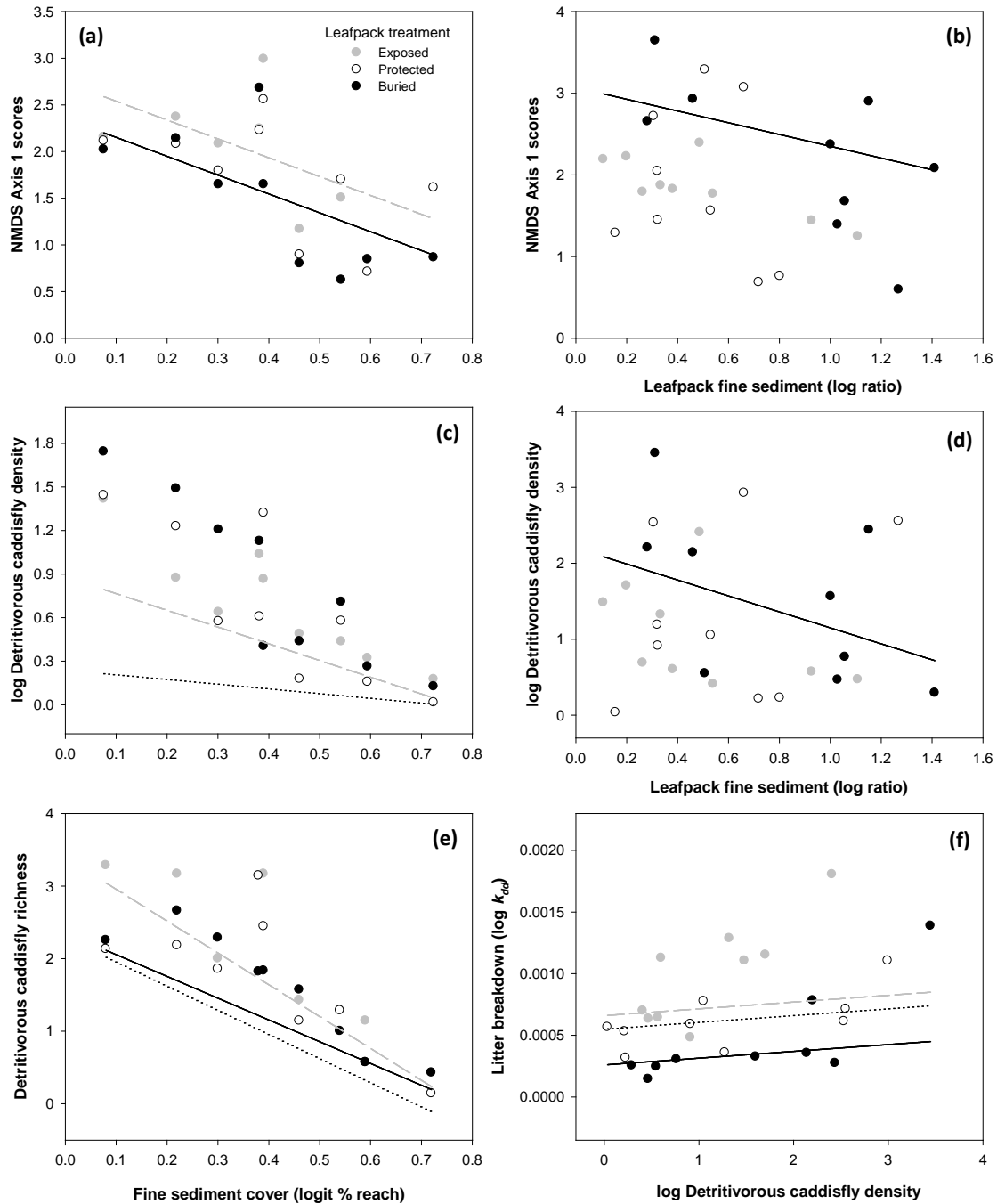


FIG. 2. Invertebrate community results from field experiment on the Canterbury Plains, South Island, NZ, testing the influence of leaf-pack treatments (exposed, protected and closed) and sediment deposition on invertebrates and decomposition of detrital resources along a sedimentation gradient in nine agricultural streams sampled during the austral summer of 2010/2011. The relationship of (a) leaf pack invertebrate community composition (un-transformed non-metric dimensional scaling [NMDS] Axis 1 scores) to deposited sediment (logit

sediment % cover), (b) community composition and the ratio of sediment (inorganic particles < 2mm) to remaining leaf litter in leaf pack treatments at Day 72, densities of detritivorous caddisflies (individuals g/AFDM litter) to (c) sediment cover and (d) the sediment ratio, (e) untransformed taxa richness (rarefied taxa g/AFDM litter) of detritivorous caddisflies to sediment cover, and (f) litter breakdown (k_{dd} , g AFDM/degree day) to densities of detritivorous caddisflies. Unless stated otherwise, mean log-transformed ($\log_{10}+1$) data is presented. Where appropriate, regression lines indicate significant influences ($\alpha = 0.05$) of sediment and leaf pack treatments. Grey-dashed line, exposed treatments; black-dotted, protected; black-solid, buried. See text and Appendix B (Tables 2-4) for statistical results.

Laboratory experiments

The two laboratory experiments indicated that deposited sediment weakened consumption rates of detritus by detritivorous caddisflies through decreased resource accessibility (Fig. 3; Appendices C and D). In Experiment 1, the sediment treatment significantly reduced total coarse particulate organic matter (CPOM) consumption by *Triplectides* (ANOVA, $F_{3,41} = 47.2$, $p < 0.001$, Tukey's HSD, $p < 0.05$, Fig. 3a), but had no effect upon leaf breakdown in the absence of this detritivore (Tukey's HSD, $p = 0.997$). Experimental treatments did not significantly affect microbial activity (ANOVA, $F_{3,41} = 1.0$, $p = 0.40$). In Experiment 2, total consumption rates of CPOM by *Triplectides* and *Olinga* declined with increasing levels of sediment (LMEM, $t_{1,41} = -5.48$, $p < 0.001$; Fig. 3b); overall, *Olinga* consumed less detritus, reflecting its smaller body mass (LMEM, $t_{1,41} = -10.15$, $p < 0.001$, Fig. 3b). However, different patterns of detrital consumption along the experiment sediment gradient were observed in *Triplectides* and *Olinga* after correcting for total invertebrate metabolic biomass. The rate of CPOM consumed per total metabolic body mass declined in *Triplectides* with increasing sediment (LMEM, $t_{1,41} = -2.56$, $p < 0.05$, Fig. 3c), and although not significant at $\alpha = 0.05$, consumption by *Olinga* appeared to increase (LMEM, $t_{1,41} = -2.04$, $p = 0.051$, Fig. 3c). In both

caddisfly treatments, microbial activity did not significantly change with sediment (LMEM, $t_{1,41} = -0.37$, $p = 0.71$).

These patterns in consumption were reflected by changes to mean individual biomass, growth rates, and % mortality of the detritivorous caddisflies in both experiments (Appendix D Tables 2 and 3, Fig. 4). Although no significant differences in mean individual biomass of *Triplectides* were found between treatments in Experiment 1 (Fig. 4a), growth rates (mg of exuviae produced per day per AFDM of metabolic body mass) were negatively affected by sediment (ANOVA, $F_{1,19} = 4.5$, $p < 0.05$, Fig. 4c). In Experiment 2, declines in growth rates were observed in both *Olinga* and *Triplectides* along the experimental sediment gradient (LMEM, $t_{1,40} = -3.72$, $p < 0.001$, Fig. 4d) and corroborating this result, percentage growth of *Olinga* estimated from the formation of newly secreted case material declined significant with sediment (LMEM, $t_{1,18} = -4.86$, $p < 0.001$). However, in Experiment 2, mean individual *Triplectides* biomass increased with sediment (LMEM, $t_{1,40} = 3.53$, $p < 0.001$), whereas mean individual *Olinga* biomass did not change significantly (Fig. 4b). In both experiments, the mortality rates of *Triplectides* increased with sediment (Appendices C and D Table 3; Fig. 4e,f), thus potentially explaining the increase in mean individual biomass along the sediment gradient in Experiment 2. This was corroborated by the increase in minimum individual biomass of *Triplectides* along the sediment gradient in Experiment 2 (LMEM, $t_{1,40} = 2.89$, $p < 0.01$); maximum individual *Triplectides* biomass showed no change (Appendix D Table 2). Moreover, sclerotized tissue recovered from microcosms and that present in stomach contents indicated that *Triplectides* may have engaged in cannibalism. In Experiment 2, the mortality rates of *Olinga* did not significantly change with sediment (GLMM, $z_{1,18} = -0.62$, $p = 0.53$, Fig. 4f).

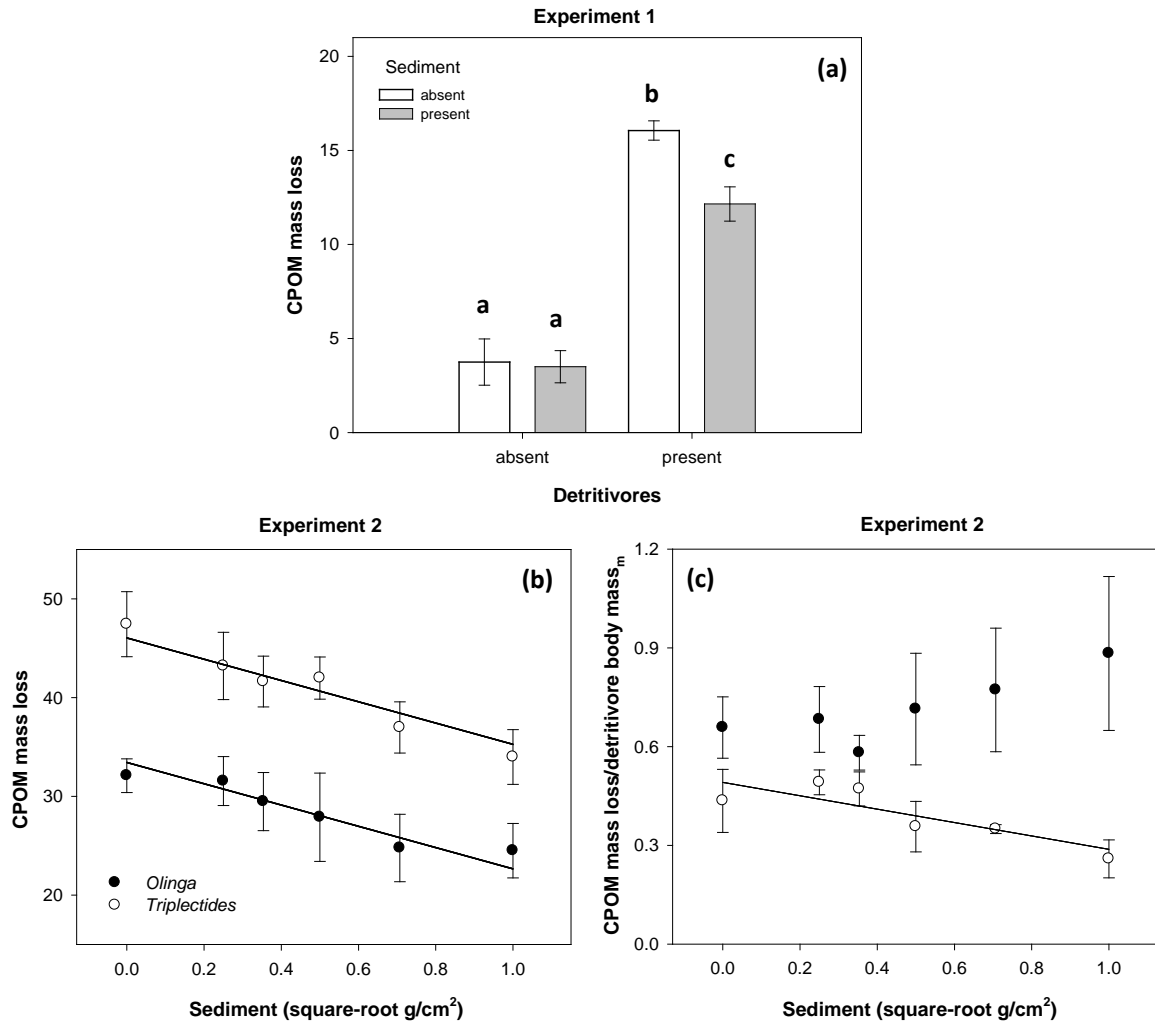


FIG. 3. Results from two laboratory microcosm experiments used to assess the effects of fine sediment deposition on invertebrate consumers and decomposition of detrital resources. (a) Experiment 1 investigated the factorial effects of sediment (grey bars) and detritivores on CPOM mass loss (mg AFDM/day). Experiment 2 revealed the effects of sediment (square-root transformed g/cm²) on (b) CPOM consumption (mg AFDM loss per day) and (c) CPOM consumption (mg AFDM loss per day) per total metabolic biomass (mg AFDM) of the detritivorous caddisflies *Olinga feredayi* (Conoesucidae) and *Triplectides obsoletus* (Leptoceridae). Bars and points show mean values (± 1 standard error). See text and Appendices C-D for statistical results.

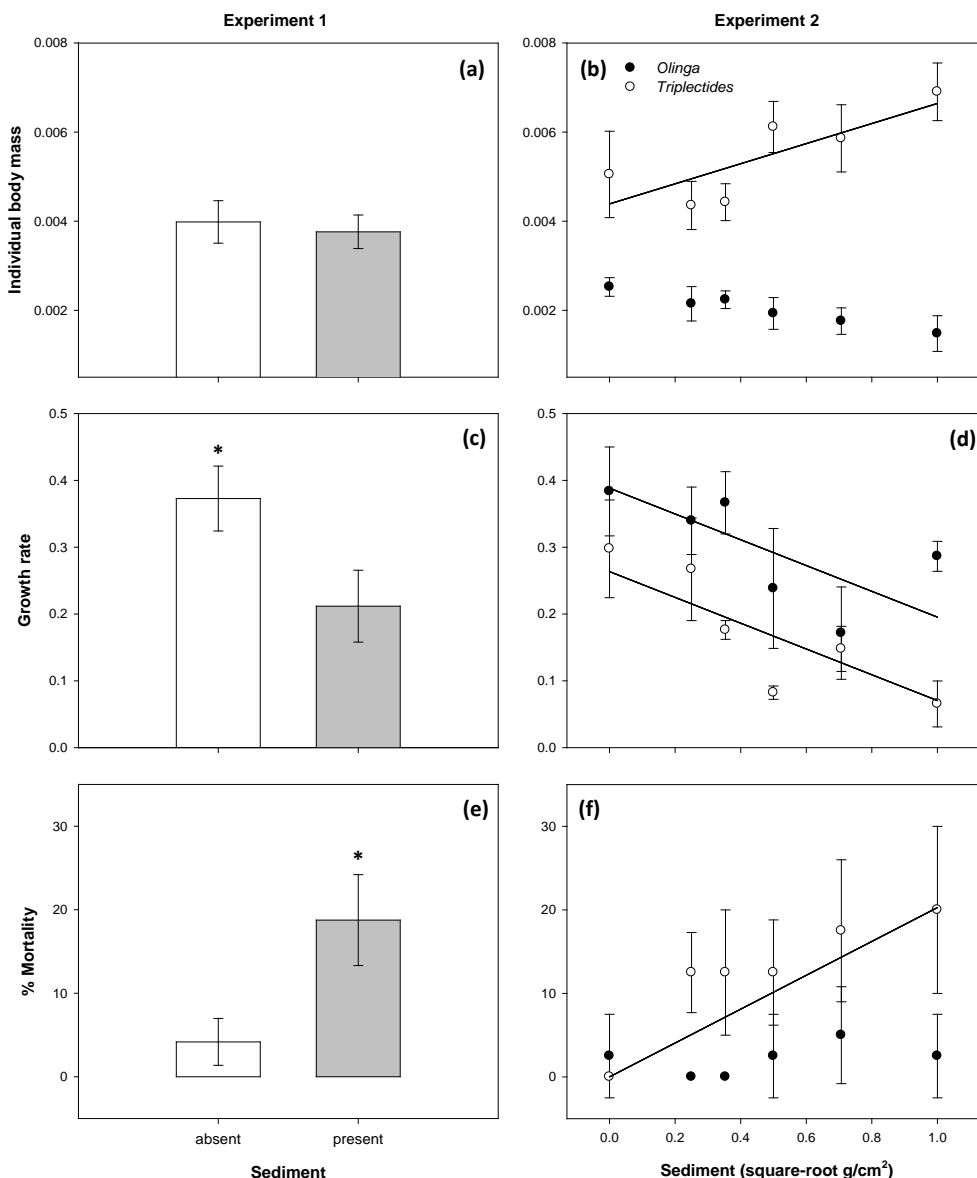


FIG. 4. Results from two laboratory microcosm experiments used to assess the effects of fine sediment deposition on invertebrate consumers and decomposition of detrital resources. Experiment 1 revealed the effects of sediment (grey bars) on (a) mean larval biomass (g AFDM), (c) growth rates (mg AFDM exuviae day⁻¹ total metabolic biomass⁻¹), and (e) % mortality of the detritivorous leptocerid caddisfly *Triplectides obsoletus*. Experiment 2 revealed the effects of sediment (square-root g/cm²) on (b) mean larval biomass (g AFDM), (d) growth rates (mg AFDM exuviae day⁻¹ total metabolic biomass⁻¹), and (f) mortality of the detritivorous caddisflies *Olinga feredayi* (Conoesucidae) and *Triplectides obsoletus* (Leptoceridae). Bars and points show mean values (± 1 standard error). See text and Appendices C-D for statistical results.

DISCUSSION

We were interested in better understanding how sedimentation affects detrital processing in streams. The influences of sediment deposition were predicted to affect consumer-resource interactions and invertebrate community composition, thus demonstrating how environmental context might modulate the importance of cross-ecosystem linkages and key ecosystem functions such as decomposition. Moreover, these changes indicate how sediment legacy effects may reduce key benefits of riparian management, particularly bankside revegetation. We hypothesized that sedimentation would alter the availability of detrital resources to stream food webs via a combination of direct (physical) and indirect (biological) effects. We found evidence of impaired litter breakdown rates, and were able to associate this with burial by sediment and reduced densities of sediment-sensitive ‘shredding’ caddisflies in the field. Laboratory experiments indicated that burial by sediment reduced resource accessibility thus causing negative effects upon functionally important stream insects. In our study, sediment influences on microbial processes were equivocal in the field and the laboratory. However, the evidence from the laboratory experiments was important for two reasons; it demonstrated how sediment weakened consumptive interactions and potentially affected energy flow, and also showed how sediment-induced changes to habitat and resource availability might negatively affect sediment-sensitive taxa. Previous studies have struggled to untangle these pathways, partly due to confounding physical effects and complex interactions with other stressors, potentially leading to compensatory effects of increased microbial processing over decreased invertebrate ‘shredding’ activity (Niyogi et al. 2003, Hladysz et al. 2010). By combining field assays that realistically incorporated ecosystem structure with complementary laboratory experiments, we were better able to elucidate mechanisms of sediment disturbance affecting detrital processing. This

approach has contributed to a better understanding of how different perturbation pathways associated with human land uses influence food-web linkages and stream ecosystem function.

Sediment impacts on detrital breakdown

The burial of organic matter by sediment can impair detrital breakdown, thus negating the effects of nutrient enrichment in modified stream ecosystems (Spänhoff et al. 2007). Decreased physical abrasion may contribute to reduced litter breakdown rates (Pascoal et al. 2005), but studies that did not control for the confounding effects of increased sediment loads during high flow events observed faster breakdown rates (Bird and Kaushik 1992, Benfield et al. 2001, Ferreira et al. 2006). In our study, we attempted to avoid these confounding physical effects and more realistically reflect ecosystem structure by using a litter breakdown assay with three different leaf pack treatments (exposed, protected, and buried). We saw evidence that the physical processes affecting litter decomposition (i.e., abrasion and burial) were likely affected by the conditions associated with sedimentation.

However, contrary to previous studies, we found weak evidence for sediment influences on microbial activity. Litter burial by sediment may create anoxic conditions and reduce the detrital surface area available for microbial colonization (Pascoal et al. 2005). McTammany et al. (2008) showed the activity of microbes on wood was negatively correlated with the amount of deposited inorganic sediment, although they used a different method to estimate respiration (i.e., CO₂ production). We did observe significantly lower rates of microbial activity in buried leaf packs across all streams, thus corroborating the findings of other studies that associated stream-bed burial of litter with lower decomposition rates, decreased microbial conditioning, and changes in the chemical composition of leaves (Herbst 1980, Danger et al. 2012). Impaired microbial processes likely contributed to these responses, and recent research has shown that

sediment was associated with altered bacterial community composition on leaves, with a greater proportion of anaerobic taxa dominating at high sediment sites (Newman 2011). This suggests that low dissolved oxygen levels within sediment affects bacterial assemblages (Newman 2011). Similarly, additions of very fine sediment slightly reduced fungal assemblage richness and the sporulation rate of three fungal species in a laboratory study (Sanpera-Calbet et al. 2012).

These studies indicate that sediment can affect bacterial and fungal communities, thus impairing the quality of detrital resources, and these changes may contribute to slower litter breakdown rates. Diversity at the microbial decomposer level can affect decomposition rates through mechanisms including facilitation and resource partitioning, although functional redundancy may limit complementarity effects of fungi in streams (Gessner et al. 2010). However, the homogenizing effects of sediment may affect the efficiency at which microbial communities degrade a wide range of litter constituents, thus contributing to impaired decomposition rates. This reflects theory proposing that resource and habitat heterogeneity can mediate the effects of biodiversity on ecosystem function through increased resource partitioning (Tylianakis et al. 2008b, Constantini and Rossi 2010). Our results, coupled with evidence from the literature, suggests that increased sedimentation can impair detrital processing by altering physical conditions and microbial communities, thus affecting breakdown rates directly (e.g., via reduced physical abrasion), and more indirectly by decreasing food resource quality for detritivores.

Sediment impacts on stream invertebrates

Our results were consistent with those of numerous other studies, which indicate that deposited sediment can have deleterious effects on invertebrate community composition (see review by Jones et al. 2012). However, less well understood is how these changes affect food-

web linkages and ecosystem functions such as decomposition. We predicted that sediment influences on community composition and resource availability affects leaf litter consumption, thus potentially weakening aquatic-terrestrial linkages. Our study indicated that sediment influences led to reduced diversity of functionally important taxa. Greater detritivore richness has been associated with faster decomposition, although equivocal responses have also been observed, explained by negative (antagonistic) species interactions (Gessner et al. 2010). We saw evidence of this with potential cannibalism by *Triplectides* in Experiment 2, which likely contributed to greater mortality and slower rates of leaf mass loss via decreased consumption with increased sediment. The minimum size of individual *Triplectides* increased along the experimental sediment gradient, suggesting that larger congeners cannibalized smaller individuals. This may help to explain why average size of *Triplectides* increased with sediment, although a release from density-dependent competition likely enhanced resource availability for remaining individuals.

Although the exact mechanisms of increased diversity remain untested, we suggest that the homogenizing effects of sediment on habitat and resources may reduce niche partitioning. This effect, coupled with lower diversity leading to reduced selection effects and facilitation, may have contributed to the association of sediment influences with slower litter breakdown. Steudel et al. (2012) showed that greater biodiversity enhanced the relative rate of ecosystem functioning with increasing environmental stress. Stream decomposition studies have demonstrated the important contribution of detritivorous invertebrates to litter breakdown (e.g., Hieber and Gessner 2002), particularly when populations are reduced by anthropogenic stress (Carlisle and Clements 2005). In human-modified catchments, potential sedimentation effects on substrate size have been associated with decreased breakdown rates and reduced densities and

biomass of detritivores (Sponseller and Benfield 2001). In our streams, the loss and degradation of habitat, coupled with the burial of detrital resources suggest stream litter decomposition may be strongly influenced by sediment legacy effects (Greenwood et al. 2012, Burdon et al. 2013). Our field assay results indicated that sedimentation reduces populations of functionally important consumers and detrital resource accessibility; it is highly likely that resource quality is also affected. Our experiments showed that detrital consumption by caddisflies was negatively affected by sedimentation; a result consistent with a previous study using hyporheic amphipods (Navel et al. 2010). This is important, because detritivorous caddisflies such as *Olinga feredayi* have been shown to be more effective at consuming detritus than other invertebrates commonly associated with high levels of deposited sediment (i.e., the snail *Potamopyrgus antipodarum* and the amphipod *Paracalliope fluviatilis*; Niyogi et al. 2003).

In our second experiment, *Olinga* appeared to consume as much or more detritus per unit of metabolic body mass with increased sediment, suggesting that detrital mass loss declined less rapidly than metabolic body mass. This implies that sediment deposition forced *Olinga* to forage less selectively on lower-quality detritus, whilst potentially also removing habitat for other food resources; *Olinga* is a facultative detritivore that also consumes biofilms (Burrell and Ledger 2003). Likewise, the reduced survival rates of *Triplectides* with increased sediment may have been influenced by the removal of habitat (reduced habitat complexity through burial by sediment), leading to increased encounter rates and/or reduced resource availability, thus causing antagonistic interactions. However, cannibalism was not density-dependent in a detritivorous North American caddisfly (Limnephilidae: *Asynarchus nigriculus*), occurring even at low densities (Wissinger et al. 1996), thus suggesting that in our experiment, reduced resource accessibility alone contributed to cannibalism. Overall, the results of our laboratory experiments

demonstrate that sediment additions can exert negative effects on detrital processing, insect growth rates, and survival, thus indicating possible mechanisms contributing to the patterns observed in the field.

Subsidy theory and environmental context

Our study has demonstrated how environmental context can influence stream invertebrate communities and their interactions with a terrestrially-derived resource subsidy (detritus). It therefore contributes to subsidy theory by indicating that an anthropogenic stressor (i.e., sediment) can modulate the availability of subsidized resources to stream food webs directly by reducing resource accessibility and indirectly through the loss of functionally important consumers. This suggests that environmental context can not only affect the magnitude of a subsidy (Paetzold et al. 2011), but can also modulate its availability to recipient consumers and food webs. Although the concept is well established (Cardinale et al. 2000), environmental context and its effect upon recipient community composition and interactions has rarely been explicitly considered in resource subsidy research. One of the few studies to investigate these effects indicated that hydrological disturbance in streams not only affected the magnitude and direction of resource subsidy inputs, but also controlled recipient consumers' numerical and functional responses by altering habitat availability (Greenwood and McIntosh 2008). Moreover, recipient species identity may influence the uptake of prey inputs and indirectly influence donor community composition, demonstrating that recipient communities are important in helping determine the strength of cross-ecosystem interactions (Romero and Srivastava 2010).

Considering the role of recipient community composition and species identity builds upon previous studies that have shown how donor community composition can affect cross-ecosystem interactions by altering the export of detritus (Mineau et al. 2012), prey (Wesner

2012), and predators (Knight et al. 2005). Likewise, studies involving the effects of anthropogenic disturbance have shown how reductions in emergent stream insect prey can lead to numerical responses by riparian predators (Paetzold et al. 2011). In our study, sediment effects may have wider food web and ecosystem consequences, and reduced abundances of emerging adult caddisflies may negatively impact riparian consumers that use this prey subsidy (Burdon and Harding 2008). However, a better understanding of how environmental context affects the strength of cross-ecosystem interactions is crucial to developing theory on resource subsidies, food-web dynamics, and ecosystem function. Moreover, given the importance of aquatic-terrestrial linkages in streams, such an understanding will better inform management about restoring cross-ecosystem interactions and detrital processing. Future studies should consider manipulating in-stream stress levels (e.g., sedimentation) whilst controlling detrital inputs (and associated riparian cover) to further investigate the wider ecosystem implications of environmental context (e.g., land use legacy effects).

Implications for management

Dealing with legacy effects from past land uses or upstream activities is a key challenge facing managers when attempting to mitigate impacts or rehabilitate degraded streams (Walsh et al. 2007). Our study demonstrates the potential for sediment legacy effects to adversely affect a purported benefit of riparian plantings, which is to increase organic habitat and enhance detrital food webs (Lake et al. 2007). Moreover, this also means that measuring the success of stream rehabilitations using functional indicators such as detrital processing may be obscured by sediment-related processes. Our results further reinforce the need to address inputs of sediment (including upstream sources) and in-stream habitat (e.g., deposited sediment) to help better realize the benefits of riparian management involving bank-side revegetation. Sediment removal

in affected reaches (Sarriquet et al. 2007) may help reconnect aquatic-terrestrial linkages through the enhancement of habitat and the re-establishment of functionally important consumers. Such measures could help enable stream rehabilitation efforts to turn the ‘field of dreams’ into reality (Sudduth et al. 2011).

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LITERATURE CITED

- Allan, D. J. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257-284.
- American Public Health Association (APHA). 1995. Standard methods for the examination of water and wastewater. American Public Health Association, Washington DC, USA.
- Baayen, R. H. 2012. “languageR” package. R Foundation for Statistical Computing, Vienna, Austria.

- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using Eigen and Eigenfaces. R Foundation for Statistical Computing, Vienna, Austria.
- Benfield, E. F. 2007. Decomposition of leaf material. Pages 711-720 in F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, Burlington, MA, USA.
- Benfield, E. F., J. R. Webster, J. L. Tank, and J. J. Hutchens. 2001. Long-term patterns in leaf breakdown in streams in response to watershed logging. International Review of Hydrobiology 86:467-474.
- Bird, G. A. and N. K. Kaushik. 1992. Invertebrate colonization and processing of maple leaf litter in a forested and an agricultural reach of a stream. Hydrobiologia 234:65-77.
- Brown, J. H., A. P. Allen, and J. F. Gillooly 2007. The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. Pgs 1-15 in Body size: The structure and function of aquatic ecosystems. A. G. Hildrew, D. G. Raffaelli and R. Edmonds-Brown (eds.). Cambridge University Press, Cambridge, UK.
- Burdon, F. J., A. R. McIntosh, and J. S. Harding. 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. Ecological Applications 23:1036–1047.
- Burdon, F. J. and J. S. Harding. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. Freshwater Biology 53:330-346.
- Burrell, G. P. and M. E. Ledger. 2003. Growth of a stream-dwelling caddisfly (*Olinga feredayi*: Conoesucidae) on surface and hyporheic food resources. Journal of the North American Benthological Society 22:92-104.
- Cardinale, B. J., K. Nelson, and M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos 91:175-183

- Carlisle, D. M. and W. H. Clements. 2005. Leaf litter breakdown, microbial respiration and shredder production in metal-polluted streams. *Freshwater Biology* 50:380-390.
- Clapcott, J. E., R. G. Young, J. S. Harding, C. D. Matthaei, J. M. Quinn, and R. G. Death. 2011. Sediment assessment methods: protocols and guidelines for assessing the effects of deposited fine sediment on in-stream values. Cawthron Institute, Nelson, New Zealand.
- Costantini, M. L., and L. Rossi. 2010. Species diversity and decomposition in laboratory aquatic systems: the role of species interactions. *Freshwater Biology* 55:2281-2295.
- Danger, M., J. Cornut, A. Elger, and E. Chauvet. 2012. Effects of burial on leaf litter quality, microbial conditioning and palatability to three shredder taxa. *Freshwater Biology* 57:1017-1030.
- Edwards, E. D. and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* 337:151-159.
- Ferreira, V., M. A. S. Graca, J. de Lima, and R. Gomes. 2006. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. *Archiv für Hydrobiologie* 165:493-513.
- Fisher, S. G. and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421-439.
- Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology and Evolution* 25:372-380.
- Greenwood, M. J. and A. R. McIntosh. 2008. Flooding impacts on responses of a riparian consumer to cross-ecosystem subsidies. *Ecology* 89:1489-1496.

- Greenwood, M. J., J. S. Harding, D. K. Niyogi, and A. R. McIntosh. 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology* 49:213-222.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95:14843-14847.
- Haynes, R. J., and G. S. Francis. 1990. Effects of mixed-cropping farming systems on changes in soil properties on the Canterbury Plains. *New Zealand Journal of Ecology* 14:73-82
- Herbst, G. N. 1980. Effects of burial on food value and consumption of leaf detritus by aquatic invertebrates in a lowland forest stream. *Oikos* 35:411-424.
- Hieber, M. and M. O. Gessner. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83:1026-1038.
- Hladyz, S., S. D. Tiegs, M. O. Gessner, P. S. Giller, G. Rîşnoveanu, E. Preda, M. Nistorescu, M. Schindler, and G. Woodward. 2010. Leaf-litter breakdown in pasture and deciduous woodland streams: a comparison among three European regions. *Freshwater Biology* 55:1916-1929.
- Jones, E. B. D., G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology* 13:1454-1465.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28: 1055–1071
- Kleiber, M. 1947. Body size and metabolic rate. *Physiological Reviews* 27:511–541.

- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880-883.
- Kominoski, J. S., and A. D. Rosemond. 2011. Conservation from the bottom up: forecasting effects of global change on dynamics of organic matter and management needs for river networks. *Freshwater Science* 31:51-68.
- Laeser, S., C. Baxter, and K. Fausch. 2005. Riparian vegetation loss, stream channelization, and web-weaving spiders in northern Japan. *Ecological Research* 20:646-651.
- Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. *Freshwater Biology* 52:597-615.
- MacLeod, C. J. and H. Moller. 2006. Intensification and diversification of New Zealand agriculture since 1960: an evaluation of current indicators of land use change. *Agriculture, Ecosystems and Environment* 115: 201-218
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140-148.
- McTammany, M. E., E. F. Benfield, and J. R. Webster. 2008. Effects of agriculture on wood breakdown and microbial biofilm respiration in southern Appalachian streams. *Freshwater Biology* 53:842-854.
- Mineau, M. M., C. V. Baxter, A. M. Marcarelli, and G. W. Minshall. 2012. An invasive riparian tree reduces stream ecosystem efficiency via a recalcitrant organic matter subsidy. *Ecology* 93:1501-1508.

Navel, S., F. Mermillod-Blondin, B. Montuelle, E. Chauvet, L. Simon, C. Piscart, and P.

Marmonier. 2010. Interactions between fauna and sediment control the breakdown of plant matter in river sediments. *Freshwater Biology* 55:753-766.

Newman, M. 2011. Molecular phylogenetic characterization of microbial community dynamics associated with freshwater stream environmental organic matter sources. Unpublished Ph.D thesis. Department of Biological Sciences, University of Auburn, Alabama, US.

Niyogi, D. K., K. S. Simon, and C. R. Townsend. 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology* 48:1698-1708.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2010. *vegan: Community Ecology Package*. R Foundation for Statistical Computing, Vienna, Austria.

Paetzold, A., M. Smith, P. H. Warren, and L. Maltby. 2011. Environmental impact propagated by cross-system subsidy: chronic stream pollution controls riparian spider populations. *Ecology* 92:1711-1716.

Parkyn, S. M. and M. J. Winterbourn. 1997. Leaf breakdown and colonisation by invertebrates in a headwater stream: comparisons of native and introduced tree species. *New Zealand Journal of Marine and Freshwater Research* 31:301-312.

Pascoal, C., F. Cássio, A. Marcotegui, B. Sanz, and P. Gomes. 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. *Journal of the North American Benthological Society* 24:784-797.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2009. *nlme: linear and non-linear mixed effects models*. R Foundation for Statistical Computing, Vienna, Austria.

- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289-316.
- Polis, G. A. and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* 147:396-423.
- Reid, D. J., P. S. Lake, G. P. Quinn, and P. Reich. 2008. Association of reduced riparian vegetation cover in agricultural landscapes with coarse detritus dynamics in lowland streams. *Marine and Freshwater Research* 59:998-1014.
- Rier, S. T. and D. K. King. 1996. Effects of inorganic sedimentation and riparian clearing on benthic community metabolism in an agriculturally-disturbed stream. *Hydrobiologia* 339:111-121.
- Romero, G. Q. and D. S. Srivastava. 2010. Food-web composition affects cross-ecosystem interactions and subsidies. *Journal of Animal Ecology* 79:1122-1131.
- Sanpera-Calbet, I., E. Chauvet, and J. Richardson. 2012. Fine sediment on leaves: shredder removal of sediment does not enhance fungal colonisation. *Aquatic Sciences* 74:527-538.
- Sarriquet, P. E., P. Bordenave, and P. Marmonier. 2007. Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River Research and Applications* 23:815-828.
- Spänhoff, B., C. Augspurger, and K. Kuesel. 2007. Comparing field and laboratory breakdown rates of coarse particulate organic matter: sediment dynamics mask the impacts of dissolved nutrients on CPOM mass loss in streams. *Aquatic Sciences* 69:495-502.

- Sponseller, R. A. and E. F. Benfield. 2001. Influences of land use on leaf breakdown in Southern Appalachian headwater streams: A multiple-scale analysis. *Journal of the North American Benthological Society* 20:44-59.
- Steudel, B., A. Hector, T. Friedl, C. Löffke, M. Lorenz, M. Wesche, and M. Kessler. 2012. Biodiversity effects on ecosystem functioning change along environmental stress gradients. *Ecology Letters* 15:1397-1405.
- Strayer, D. L. and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* 29:344-358.
- Sudduth, E. B., B. A. Hassett, P. Cada, and E. S. Bernhardt. 2011. Testing the field of dreams hypothesis: functional responses to urbanization and restoration in stream ecosystems. *Ecological Applications* 21:1972-1988.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ripley, B., B. Venables, K. Hornik, A. Gebhardt, and D. Firth. 2013. Package “MASS”. R Foundation for Statistical Computing, Vienna, Austria.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008a. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A. M. Klein, N. Buchmann, J. Perner, and T. Tscharntke. 2008b. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol* 6:e122.
- Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202-205.

- Walling, D. E. 1990. Linking the field to the river: Sediment delivery from agricultural land. Pages 129-152 in J. Boardman, I. D. L. Foster and J. A. Dearing (editors). Soil erosion on agricultural land. John Wiley, Chichester, UK.
- Walsh, C. J., K. A. Waller, J. Gehling, and R. M. Nally. 2007. Riverine invertebrate assemblages are degraded more by catchment urbanisation than by riparian deforestation. *Freshwater Biology* 52:574-587.
- Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge, UK.
- Warton, D. I. and F. K. C. Hui. 2010. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3-10.
- Wesner, J. S. 2012. Predator diversity effects cascade across an ecosystem boundary. *Oikos* 121:53-60.
- Wissinger, S. A., G. B. Sparks, G. L. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. *Ecology* 77:2421-2430.
- Wood, P. J. and P. D. Armitage. 1999. Sediment deposition in a small lowland stream - Management implications. *Regulated Rivers: Research and Management* 15:199-210.
- Yule, C. M., L. Boyero, and R. Marchant. 2010. Effects of sediment pollution on food webs in a tropical river (Borneo, Indonesia). *Marine and Freshwater Research* 61:204-213.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix A

Detritivorous caddisfly taxa.

Appendix B

Results from leaf-pack analyses.

Appendix C

Results from Experiment 1 randomized-block ANOVAs.

Appendix D

Results from Experiment 2 analyses (LMEM and GLMM).

CHAPTER 5

SYNTHESIS: SEDIMENTATION AND THE STRUCTURE AND FUNCTIONING OF STREAM COMMUNITIES

My thesis has addressed the potential influences of stream sedimentation at multiple levels of biological organisation (e.g., communities, food webs, and ecosystems). I postulated that sediment deposition would cause environmental stress by making habitat and associated food resources (e.g., cobbles with periphyton and leaves) less available, and potentially lead to increased substrate instability, thus contributing to changes at the community level (i.e., macroinvertebrate communities). These influences of sedimentation might also be propagated to higher levels of biological organisation including food webs and ecosystem processes. I found evidence that sediment-induced change to resource availability influenced non-linear responses (i.e., thresholds) by invertebrate communities through the degradation of habitat (Chapter 2), shifts in invertebrate-feeding traits and basal resources, leading to functionally less diverse food webs (Chapter 3), and as a net consequence, impaired ecosystem function, demonstrated by a reduction in litter breakdown rates (Chapter 4).

Sediment impacts across multiple levels of biological organisation

In my first chapter, I reviewed the literature on impacts of sediment on stream ecosystems. This chapter highlighted inorganic fine sediment pollution as a pervasive problem globally, and in particular, as a major pathway whereby agricultural land uses stress aquatic ecosystems. In Chapter 1, I discussed the concept of ‘assimilative capacity’, whereby if sediment inputs exceed the natural ability of a stream ecosystem to process such material (e.g., through benign storage, mobilisation, and transport), then ‘sedimentation’ would occur, with concomitant ecological changes (Cairns 1977, Waters 1995). Importantly, sediment deposition alters

ecosystem structure by changing habitat and reducing substrate stability, thus causing direct and indirect effects across multiple trophic levels. These changes were predicted to have implications for higher levels of biological organisation (e.g., food webs and ecosystems). At the basal level, sediment can decrease primary production leading to the dominance of heterotrophy, although detrital pathways can also be affected by impaired microbial activity and reduced resource availability via burial. Numerous studies have recorded adverse effects of sedimentation on stream invertebrates, including reduced abundance and biomass with shifts in community composition from EPT-dominated assemblages (Ephemeroptera, Plecoptera, Trichoptera) to communities characterised by worms, snails and micro-crustaceans (Waters 1995). Such shifts may reflect a non-linear effect of sediment, but community sediment thresholds have only been reported in a few studies (Table 1), and the underlying mechanisms have not been adequately determined (see Chapter 2). However, Lenat et al. (1979) described the situation where sedimentation exceeded the ‘assimilative capacity’ of a stream as the difference between ‘habitat reduction’ and ‘habitat change’, thus suggesting sediment impacts on stream fauna may be mediated through habitat degradation and loss. Sediment-induced changes in invertebrate prey have been related to impacts on fish communities, with reduced densities and biomass a commonly reported response found in the literature (e.g., Waters 1982). Thus, faunal reductions caused by sediment within a trophic level may affect the next level via diminished transfers of energy. These effects have the potential to propagate beyond traditional stream boundaries, affecting riparian predators and reciprocal linkages of prey.

In Chapter 1, I applied sediment literature to several ecological theories to make predictions about impacts of this stressor (sedimentation) at the food-web level. Several important predictions were made; although sediment was expected to reduce ecosystem

productivity, food-chain length may be a poor indicator of change. However, functional-feeding groups that integrate different energetic pathways can be disproportionately affected by sediment, thus leading to simpler food webs (Yule et al. 2010). Such effects potentially lead to decreased ecosystem function, and asymmetric food-web linkages that may contribute to reduced system stability (Rooney et al. 2006). In particular, sediment was predicted to affect specialized consumers, including grazing herbivores, obligate ‘shredders’ and filter-feeding collectors more strongly than detritivorous deposit-feeders, meaning trophic pathways in stream food webs were likely altered (Chapter 1 Figure 3). Food-web theory suggests that reductions in resource availability with environmental stress favour dietary generalists, showing increased polyphagy and omnivory, and thus creating highly interconnected food webs (Woodward and Hildrew 2002). However, changes in invertebrate traits (e.g., size, burrowing ability, and degree of armouring) induced by sediment were also predicted to lead to food-web compartmentalisation, owing to lower availability of prey to larger consumers (e.g., fish). Despite the overall reduced ecosystem productivity and the apparent ‘bottom-up’ effects of sedimentation on higher trophic levels, it was considered that spatial subsidies of invertebrate prey from the adjacent riparian zone and unaffected upstream tributaries might help offset decreased benthic prey availability. These subsidies could help sustain ‘top-down’ predation by large mobile predators (i.e., fish) on more vulnerable benthic prey, and might sustain food-chain length despite the reduced availability of aquatic prey. Overall, however, sediment was expected to lead to functionally less diverse and simpler food webs (see Chapter 3), suggesting that changes at the community level might influence ecosystem processes such as detrital processing (see Chapter 4).

Deposited sediment thresholds

In Chapter 2, I reported results from a survey of 30 streams representing gradients of deposited sediment and dissolved nutrients (i.e., nitrate). Although there is a plethora of studies showing that benthic invertebrate communities change with the degree of sedimentation (Jones et al. 2012), less well understood are the potential non-linear responses (i.e., sediment thresholds) and their underlying mechanisms (Burdon et al. *in press*). Moreover, theoretical and empirical studies of habitat loss have indicated that scalar effects are common (Homan et al. 2004), suggesting that spatial context may influence threshold values. In Chapter 1, I collated deposited-sediment thresholds reported in the literature, and concluded that spatial scale of sampling could influence sediment threshold values (see Table 1). Although there is a strong relationship between substrate composition and invertebrate distribution at the patch scale (Culp et al. 1983), these are often not obvious when sampling whole reaches (Larsen et al. 2009). Thus, the scaling up of impacts from the patch scale may be problematic due to difficulties of quantifying sediment stress at larger spatial scales, meaning the most appropriate sampling resolution used to detect impacts on macroinvertebrates is an important issue (Jones et al. 2012). Despite this, few researchers have considered the spatial scale of sampling when reporting potential sediment thresholds.

My results in Chapter 2 provide a better understanding of how spatial scale might affect sediment threshold values, and I suggest more robust values for management purposes. Importantly, pollution-sensitive invertebrates (% EPT) demonstrated a strong non-linear response to sediment, and change-point analysis indicated marked declines beyond a threshold of approximately 20% fine sediment cover at the reach scale (30 m). A lesser value of 13% was elucidated at the patch scale (0.0625 m^2), corroborating lower figures recorded by previous

TABLE 1. Published deposited sediment thresholds for benthic invertebrate communities in streams and rivers at two spatial scales, reach and patch. % Sed., the relative proportion of deposited fine inorganic sediment (<2 mm grain size); SS, sediment-sensitive taxa; EPT, pollution-sensitive stream-insect orders (Ephemeroptera, Plecoptera, Trichoptera); interstitial sediment, sediment as a proportion of total substrate mass (in contrast to % cover stated in other examples). Highlighted in grey are my findings from Chapter 2.

Scale	% Sed.	Country	Region	Reference	Comments
Reach	9.7	USA	Western States	(Bryce et al. 2010)	Survey, 8 SS taxa
	14.8	Canada	New Brunswick	(Benoy et al. 2012)	Survey, %EPT
	19.6	USA	Southwestern States	(Jessup et al. 2010)	Survey, 'Mountain' streams, SS 'clinger' taxa
	21	NZ	Canterbury Plains	(Burdon et al. <i>in press</i>)	Survey, %EPT
	30	USA	Pacific Northwest and Idaho	(Relyea et al. 2000)	Survey, absolute limits, 7 SS taxa
Mean	19.0				
Patch	5	NZ	Otago	(Wagenhoff et al. 2012)	Experiment, EPT densities
	7.1	UK	Wales	(Larsen et al. 2009)	Survey, median EPT taxa, 50% abundance,
	13	NZ	Canterbury Plains	(Burdon et al. <i>in press</i>)	Survey, %EPT
	13.3	Canada	New Brunswick	(Benoy et al. 2012)	Survey, %EPT, interstitial sediment
	14.5	NZ	Otago	(Ryder 1989)	Experiment, 1 SS taxon, interstitial sediment
Mean	10.6				

researchers at a finer spatial scale (Table 1). My figures both fell within the range of previously reported thresholds, but by directly comparing patch- and reach-scale data, I was able to demonstrate the importance of spatial scale in influencing habitat thresholds (Table 1). My results differed from those of Larsen et al. (2009), who found little congruence between potential effects of sediment at two different spatial scales in Welsh upland streams. This difference may have reflected the low-gradient and predominately spring-fed nature of the streams I sampled, which are also often channelised. Channel straightening of agricultural streams can lead to a more diffuse and homogenous distribution of fine sediment on the streambed (Harrison et al. 2004).

Although threshold values are useful for management purposes, understanding the underlying mechanisms will better advance theory on sediment impacts in streams. Using structural equation modeling, I showed that decreased habitat availability (i.e., reduced coarse substrate and associated interstices) likely had a strong influence on the relative abundance of pollution-sensitive invertebrates (EPT). This finding suggested that habitat loss may be a strong determinant of the sediment threshold shown in Chapter 2. The regime shift of community composition may be linked to changes in key variables linked to ecological resilience (Pardini et al. 2010), and threshold effects of habitat loss have been shown theoretically using percolation modeling (Homan et al. 2004). Percolation models demonstrate how as the percentage of habitat lost increases, patch size decreases and isolation increases in a non-linear fashion (Homan et al. 2004). These relationships indicate why the relationship between habitat loss and sediment-sensitive invertebrates might similarly demonstrate pronounced thresholds. Importantly, the capacity of a community to recover from local reductions in diversity is dependent upon the total species pool at larger spatial scales (Fahrig 2003). Species abundance and diversity can often be

determined by the amount of suitable habitat at the patch scale, whereas immigration rates are often dependent on the total pool of colonists at the 'landscape' scale (Pardini et al. 2010).

These effects suggest that synergies between habitat loss and hydrodynamic disturbance may exist, if invertebrate community resilience is impacted by sedimentation through the removal of refugia. A scenario of this kind reflects the predictions made in Chapter 1 (Figure 1c), and is supported by experimental evidence suggesting that loss of habitat through sedimentation may be a precursor to the potential interactive effects sediment and hydrodynamic disturbance. (Bond and Downes 2003). However, increased substrate instability may cause environmental stress under base-flow conditions, reflecting an unseen consequence of sediment deposition using static measures such as percentage cover. For example, Culp et al. (1986) showed that the addition of sediment to riffles with sufficient tractive force to induce transport by saltation (sliding and bouncing of sediment) created a physical disturbance that reduced total benthic densities by >50% and significantly influenced invertebrate community composition. This physical effect may have contributed to the lower sediment threshold (13%) I found at the patch scale (Chapter 2), because quantitative macroinvertebrate sampling was done in the thalweg of the channel (i.e., increased flow velocities). For this reason, I indicated in Chapter 2 that lower thresholds might be more useful where sediment fluxes are dynamic (Burdon et al. *in press*). However, it is likely that the depositional zones at stream margins and in macrophyte beds not quantitatively sampled (i.e., at the patch scale) also contributed to the greater sediment value (21%) I recorded at the reach scale (Table 1). Moreover, where samples are collected from a stream reach, the community can be composed of animals from both depositional (e.g., sediment) and erosional (e.g., cobble) patches (Jones et al. 2012), meaning that sediment thresholds may become less evident, particularly where sediment deposition is heterogeneous.

The increased emigration rate of stream invertebrates through sediment-induced ‘drift’ may contribute to decreased abundances and diversity of stream invertebrates (Jones et al. 2012). This can be a response to direct sediment stress, or unfavorable habitat conditions (Ryder 1989, Molinos and Donohue 2009). It is likely that increased ‘drift’, exacerbated by sediment-induced habitat loss, exerts an insidious effect on stream invertebrate communities, because recolonisation is reduced by the persistent sediment ‘press’ disturbance (e.g., Chapter 1, Fig 1b). For example, the experimental addition of fine sediment to a Canadian river channel yielded significantly higher rates of invertebrate drift compared to a control (Rosenberg and Wiens 1978). However, no significant difference was found in total invertebrate density following sediment addition, but this may have reflected the short duration and small scale of the manipulation. The resilience of the invertebrate community in the above example highlights how deposited sediment may provide a better indication of persistent effects on stream biota. However, most current management guidelines are based on suspended sediment targets, and thus are unlikely to be appropriate for invertebrate communities (Jones et al. 2012). A better understanding of the relationship between deposited sediment and stream invertebrates, and how environmental context (e.g., spatial scale and hydrodynamic stress) modulates these effects is critically important for validating correlative sediment thresholds with experimentation and predictive modeling.

Sediment influences on stream food webs

In Chapter 1, I noted that although sediment effects on aquatic biota are well recognized, it remains poorly understood how these changes influence stream food-web properties. In Chapter 2, I demonstrated strong influences of sediment on community composition with threshold responses, but ascertained little of the functional consequences. To address these gaps

in our knowledge, I used metrics based on stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) obtained from tissue samples of invertebrates and fish to describe structural patterns in stream food webs along the sedimentation gradient in 12 agricultural streams (Chapter 3). These metrics indicated that trophic diversity decreased along the sediment gradient, and that a strong manifestation of this change was a reduction in the consumer $\delta^{13}\text{C}$ range, thus suggesting that shifts in invertebrate community composition and reduced resource heterogeneity contributed to a ‘compression’ of trophic niche space.

Niche-space compression likely reflected the effects of sediment disturbance, which reduced specialist consumers (‘grazers’ and ‘shredders’) and led to a greater reliance on detritus (e.g., fine particulate organic matter and associated microbial communities), although isotopic mixing-model analyses were only able to discriminate reliance on periphyton or plant detritus; a gap addressed in Chapter 4. These results were consistent with those of Yule et al. (2010) who found that sedimentation created simpler food webs, with the loss of key functional-feeding groups that integrate different energetic pathways (Yule et al. 2010). Similar studies have shown that reduced resource availability may influence trophic diversity, thus leading to simpler and more interconnected food webs where polyphagy and omnivory are common (Woodward and Hildrew 2002). In my study, it was not clear whether the increasing trophic equivalence of primary consumers was due to increased polyphagy (niche ‘generalists’, Chapter 3 Fig.1b), or a stronger reliance on fine particulate organic matter (niche ‘homogeneity’, Chapter 3 Fig.1c). These two mechanisms are not mutual exclusive, and the increased proportion of collectors and deposit-feeders indicated that both mechanisms might be applicable with increased sediment. Similar to the study by Yule et al. (2010), I found evidence of niche ‘elimination’ (Chapter 3 Fig. 1d), and the loss of the algal-grazing rheophilic caddisfly *Helicopsyche* was a notable example.

The consequence of a reduction in trophic diversity was predicted to lead to decreased ecosystem function through reduced niche partitioning; further investigated in Chapter 4. Ecosystem stability may be reduced if the increasingly simplified food webs possess stronger linkages to specific resources (i.e., fine benthic organic matter), but this contention was not investigated, and increased physical disturbance may override any effects of resource homogeneity in influencing the temporal stability of communities. However, the changes to food webs in Chapter 3 may have been influenced by the convergence of the trophic niche with other dimensions of the fundamental niche. Although sediment strongly influences stream invertebrate community composition through deterministic processes (e.g., niche availability), consumers appeared to become trophically more equivalent, indicating that neutral dynamics may affect food webs where environmental stress dominates and resource heterogeneity is reduced. Alternatively, increased trophic equivalence as shown by the compression of isotopic niche space and a narrowing of the $\delta^{13}\text{C}$ range might indicate increased horizontal interactions, thus potentially leading to competitive exclusion. However, competitive interactions are predicted to be reduced under increasing physical disturbance (Peckarsky 1983, McAuliffe 1984, Poff and Ward 1989). Although there is evidence to suggest that interactions may be strengthened following perturbations (Thomson et al. 2002), our understanding of how and if this relates to competitive exclusion is limited (Holomuzki et al. 2010).

Sediment influenced invertebrate taxa richness, although much of the latter effect was due to reduced abundances of invertebrates, corroborating previously reported results using rarefied taxa richness in response to sediment effects (Vasconcelos and Melo 2008). Theoretical models explaining the relationship between disturbance and diversity have assumed that competitive exclusion occurs more rapidly when populations have high growth rates and are

large; whereas disturbance typically reduces population sizes (Huston 1994). Assuming the interval between disturbances is less than the time taken to reach competitive exclusion, equilibrium conditions will not be reached and high levels of diversity will actually be maintained (Huston 1994). A dynamic equilibrium may help explain why after rarefaction, I observed no change in taxa richness along the sediment gradient, although deterministic processes (e.g., niche availability) indicated some species turnover (i.e., influence of sediment on invertebrate community occupancy data using variation partitioning). Moreover, patch dynamics likely contribute to diversity patterns in streams. Although competitive exclusion may occur patchily, certain conditions in other patches might offset competitive effects, or more simply, reflect the highly mobile nature of most stream invertebrates (Death and Winterbourn 1995). However, widespread empirical evidence is still lacking for the general application of diversity models in stream ecosystems (Tonkin and Death 2012), and Death (2010) admonished stream ecologists for using models from other fields of ecology that did not accurately reflect lotic conditions.

Nonetheless, in their review of diversity models, Petraitis et al. (1989) suggested that the nature of the relationship between disturbance and diversity depends on the balance between immigration and extinction rates as patch recolonisation proceeds following a disturbance. This postulate is conceptually similar to the neutral models derived from Hubbell's unified neutral theory of biodiversity (Hubbell 2001). The latter theory suggests that trophically similar taxa are equivalent and changes in diversity are stochastic, thus representing a null hypothesis to niche theory (Hubbell and Lake 2002). The unified neutral theory has been contentious amongst ecologists (McGill 2003), but there is a growing appreciation that niche and neutral processes can operate together to influence streams communities (Thompson and Townsend 2006), and

both may have a role in community ecology (Leibold and McPeck 2006). This is important, because my results in Chapters 2, 3, and 4 all show a strongly deterministic effect of sediment on community composition. However, distinguishing differences in changes to structural and functional biodiversity may better enable ecologists to make predictions about the consequences of disturbance at higher levels of organisation (e.g., food webs and ecosystems). Although one needs to be wary of how much inference to take from stable isotope data, my findings in Chapter 3 indicate that deterministic processes (e.g., niche availability) may be strongly linked to increasing trophic equivalence. Reconciling this apparent contradiction may lie in considering the greater neutrality of invertebrate functional roles, thus affecting community trophic niches as they converge with other dimensions of the fundamental niche (e.g., niche determinism strongly influenced by sediment). Thus, my results in Chapter 3 indicate that niche and neutral processes need to be considered jointly when explaining the underlying mechanisms shaping community diversity and food-web structure (Leibold and McPeck 2006).

In contrast to the strong effect of sediment on the narrowing consumer $\delta^{15}\text{C}$ range, both food-chain length (measured by maximum trophic position) and invertebrate $\delta^{15}\text{N}$ range showed no significant association with increasing sedimentation (Chapter 3). This lack of association reflected the weak influence sediment had on fish community composition, and turnover of predatory invertebrate taxa may have been sufficient to help maintain vertical structure in stream food webs along the sediment gradient. The latter contention fits predictions that species replacements can maintain trophic structure along environmental gradients in freshwater ecosystems (Leibold et al. 1997). Moreover, variability in the trophic position of fish may be attributed to three mechanisms (Post and Takimoto 2007): addition or removal of predators, changes in trophic omnivory by top predators, or changes in the trophic position of intermediate

predators. I found no evidence that any of these mechanisms influenced fish trophic position along the sediment gradient. Similarly, Anderson and Cabana (2009) found that trophic position of fish was not affected by environmental stress or the proportion of predatory invertebrates in the food web (Anderson and Cabana 2009), thus supporting the assertion that food-chain length is an insensitive indicator of change to disturbance (Walters and Post 2008).

Large mobile predators may be less sensitive to the effects of benthic disturbance in streams, particularly where spatial subsidies of prey help offset decreased stream production (Scrimgeour and Winterbourn 1989, Yule et al. 2010). In contrast, food-chain length appeared to be correlated with dissolved reactive phosphorus, indicating that fish trophic position was influenced by the effect of stream productivity (i.e., phosphorus-limited) on maximum body size attainable by a common predator, the short-fin eel (*Anguilla australis*). Although it is plausible that productivity influenced food-chain length in my study streams, this association does not imply causality, and it may have been correlated with other unmeasured variables such as distance downstream from stream source (e.g., headwater springs) or resource quality (N: P stoichiometry) that may have also affected predator body size. Previous studies have shown that predator body size is strongly correlated with trophic position (Jennings et al. 2001).

My results presented in Chapter 3 suggested that fish trophic diversity was lowest at intermediate levels of sediment despite the ranges of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showing linear declines. These results suggest that density-dependent competition may lead to trophic equivalence as fish compete for declining or more homogeneous resources, and corroborate results from experimental studies of sediment deposition on predatory fish responses (Suttle et al 2004). Using data from the sites where I recorded fish abundances indicated lower densities of stream fishes with increasing sediment. At the highest levels of deposited sediment, reduced density and

richness may have allowed remaining fish to better partition the diminishing trophic niche space. However, more research is required to better understand how habitat altered through sediment deposition affects biotic interactions in New Zealand streams. Increased sediment supply and deposition, affecting habitat, may make conditions more suitable for predators, competitors, and pathogens (White and Harvey 2001, Fausch et al. 2002, Anlauf and Moffitt 2010), and is therefore of relevance to the conservation of freshwater organisms.

Although stable isotopes can describe the trophic niche, thus making them useful to characterize food-web structure and function, there remain several caveats as discussed in Chapter 3. One potential problem is the influence of biogenic methane, which can lead to extremely depleted $\delta^{13}\text{C}$ in stream consumers (Jones and Grey 2011), and thus may confound the predictions made in Chapter 3 (Fig. 1). A better understanding of how biogeochemical processes and organism biology interact to influence ratios of stable isotopes will greatly enhance the utility of this method in freshwater ecological studies. Nonetheless, my results obtained using stable isotopes (Chapter 3) help to advance sediment research by providing a more complete functional description of stream communities. They go further than traditional indices in showing the potential consequences of sedimentation, and the ‘compression’ of trophic niche space, suggesting simpler food webs corroborated the results of previous studies (Yule et al. 2010). Although further validation of trophic patterns using traditional methods (e.g., gut-contents analysis) and experimentation are required, my results support those in Chapters 2 and 4, and strengthen the suggestion that sedimentation affects stream communities through reduced resource availability (degradation of habitat and associated carbon sources).

Sediment influences on ecosystem function: detrital processing

In Chapter 3, I showed evidence that the reliance of primary consumers on periphyton decreased as sediment increased, thus implying a greater use of detrital resources. However, although invertebrates that specialised more on ‘shredding’ coarse detritus appeared to also decline with increasing sediment, I could not discriminate potential detrital resources (e.g., fine benthic organic matter and leaf litter) using isotopic mixing-models analyses. However, sediment may impair coarse detrital consumption by ‘shredding’ invertebrates through the burial of detrital resources, making them less available (Navel et al. 2010), whereas the increased abundance of deposit-feeders may reflect the presence of more abundant fine benthic organic matter and associated heterotrophs (Nuttall and Bielby 1973, Winterbourn 2000). The patterns in Chapter 3 suggested that increased trophic equivalence (i.e., niche ‘generalists’) as a result of increased environmental stress, coupled with an increased availability of fine benthic organic matter (i.e., niche ‘homogeneity’) may have contributed to the simplification and increasing trophic equivalence of consumers along the sediment gradient. Theory predicts that resource and habitat heterogeneity may modulate the relationship between biodiversity and ecosystem functioning through niche partitioning (Tylianakis et al. 2008), thus changes in resources and communities of consumers may affect detrital breakdown (Gessner et al. 2010). These predictions, coupled with the biotic responses to sediment in Chapter 3 (i.e., loss of functional diversity) suggested sedimentation would lead to slower litter breakdown.

Streams in agricultural landscapes are often affected by habitat degradation through the removal of riparian vegetation and increasing inputs of diffuse pollutants (e.g., fine inorganic sediment). Changes to environmental context (stream and riparian habitat) induced by human land uses were considered important, because although revegetation of riparian zones can help

mitigate agricultural impacts, sediment pollution can have continuing legacy effects reducing the availability of terrestrial detritus through burial and by altering stream invertebrate diversity and community composition, thus leading to impaired detrital processing. To investigate the predicted effects of sedimentation on the consumption of coarse organic matter (i.e., leaves), I tested detrital processing along a sediment gradient using a litter-breakdown assay with different leaf-pack treatments in nine agricultural streams in my study region, and conducted laboratory experiments using leaf-filled stream microcosms and detritivorous caddisfly larvae (Trichoptera).

Consistent with my findings in Chapters 2 and 3, I found decreased abundances of detritivorous caddisfly larvae and slower detrital processing rates along the sediment gradient. In contrast to the results in Chapter 3, however, there was a negative effect of sedimentation on biodiversity (e.g., taxonomic richness) in leaf packs that was not explained by reduced invertebrate abundance. Sedimentation may have disproportionately affected the invertebrates associated with leaf litter, a resource that serves as both habitat and food (Death 2000). Alternatively, increased sediment may have reduced the quality and availability of the resource, thus contributing to a less productive patch, and therefore influencing diversity. In contrast to physical disturbance, which removes taxa, productivity may set an upper limit to richness (Tonkin and Death 2012).

It is likely that changes to invertebrate communities in response to increased environmental stress contributed to decreased ecosystem function (e.g., litter breakdown), as demonstrated by other studies of the effects of stream pollution (Carlisle and Clements 2005). I conducted two laboratory experiments using sediment additions to leaf-filled stream microcosms which indicated that consumer-resource interactions were particularly important for litter breakdown. However, sediment burial of litter resources had little discernible effect on microbial

activity, although other studies have reported reduced respiration and altered community composition with increasing sedimentation (McTammany et al. 2008, Newman 2011). Nonetheless, in Chapter 4, the experimental burial of coarse detritus by sediment made it less available to the detritivorous larvae of the caddisflies *Olinga feredayi* (Conoesucidae) and *Triplectides obsoletus* (Leptoceridae), thus reducing rates of litter breakdown and larval growth. These results paralleled those of Rounick and Winterbourn (1983), who showed that physical perturbation (i.e., hydrodynamic disturbance) reduced the availability of detritus through bed movement, and led to lower retention of detritus on the streambed. In part, this explained the absence of an obligate ‘shredder’ in the more disturbed stream, and contributed to slower overall breakdown of leaf litter, despite the potential for greater mechanical breakdown with increased flow perturbations (Rounick and Winterbourn 1983). My experimental results reported in Chapter 4 indicate that physical processes that reduce the availability of detrital resources and alter functional diversity lead to weakened consumption and slower litter breakdown rates.

Although sediment appeared to weaken certain consumer-resource interactions (e.g., reliance on periphyton [Chapter 3], consumption of detritus [Chapter 4]), it also had the potential to strengthen biotic interactions (e.g., implied competition between stream fishes at intermediate levels of deposited sediment [Chapter 3], and cannibalistic interactions between detritivorous caddisflies [Chapter 4]). These examples reiterate the point made in Chapter 1 that models predicting the weakening of biotic interactions across environmental stress gradients, such as the harsh-benign hypothesis (Peckarsky 1983), may be overly simplistic. In contrast, using food webs to understand the shifting strength of interactions and their functional consequences may be a more useful approach for describing and predicting changes to community structure following perturbations (Menge 1995). Food webs may be stabilized through many weak trophic links, but

where perturbations remove weak interactions and amplify those remaining, decreased persistence and stability of trophic networks may result (McCann et al. 1998, O'Gorman and Emmerson 2009). Future studies should consider how stream biodiversity affects food-web dynamics and ecosystem processes, because species losses due to perturbations such as sedimentation are likely to be non-random and may affect ecosystem functioning (Woodward 2009, Burdon et al. *in press*).

Examining the role of sedimentation and its effects upon stream biodiversity is crucial for understanding their effects on food webs and ecosystems. Some of these effects are likely to result from sedimentation through decreased substrate stability (e.g., disturbance, see earlier discussions) and increased habitat homogeneity. A number of studies have shown the importance of substrate heterogeneity, which has a strong positive correlation with diversity (Poff and Ward 1990), and has often been attributed to a “greater number of niches” in more heterogeneous habitat (Beisel et al. 2000). Increased habitat heterogeneity can have important ecological consequences, such as decreasing temporal variability in stream invertebrate populations, which nearly halved along a gradient of increasing substrate heterogeneity (Brown 2003). These effects and those discussed earlier may contribute to reduced ecosystem function by altering biodiversity and species interactions (Woodward 2009). This is particularly important to litter breakdown, because laboratory studies have shown that increased diversity of detritivores can influence decomposition through increased resource heterogeneity, thus promoting the effects of fungal diversity through reduced competition and greater niche complementarity (Costantini and Rossi 2010).

Overall, my results presented in Chapter 4 indicate that sedimentation directly and indirectly affects detrital processing through changes to resource availability and invertebrate

community composition. Future research needs to consider how sediment impacts microbial and fungal communities, and what the consequences are for litter decomposition, including within- and between trophic level interactions. Such studies will contribute to a more complete understanding of how environmental context (e.g., sedimentation) affects cross-habitat interactions and fundamental ecosystem processes such as detrital breakdown.

MANAGEMENT IMPLICATIONS

Sediment dynamics and ecosystem engineers

Ecosystem engineers may modulate sediment effects on stream communities by further influencing the environmental context under which sedimentation occurs. Ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms through the physical modification, maintenance and creation of habitat (Jones et al. 1994); their influence can be positive or negative (Jones et al. 1997). Although the concept has been criticized for being overly reductionist (at some level *all* organisms are engineers), it is still useful to consider the important effects that influential organisms have upon their surrounding environments (Wright and Jones 2006). Ecological theory describes two types; autogenic engineers that transform the environment by modifying themselves, and allogenic engineers that modify the surrounding environment by mechanically changing materials (Jones et al. 1997). The two categories are not mutually exclusive, as demonstrated by riparian trees which can both influence stream habitats through self-modification (shading of the channel) and by contributing large woody debris that serves as structure for stream organisms and changes stream morphology. Examples of allogenic engineering also include the bioturbation of benthic habitats and the removal of fine sediment by a variety of organisms including salmonids, crustaceans, and insects (Statzner 2012). Some of these activities can have negative effects on stream ecosystems. For

example, there is growing concern about the effects the invasive signal crayfish (*Pacifastacus leniusculus*) is having on freshwaters in the United Kingdom, particularly through its burrowing behaviour and effects on sediment dynamics (Harvey et al. 2011).

Submerged and emergent macrophytes in streams and rivers potentially influence the effects of sediment through habitat creation and modification, and may have positive or negative effects on stream ecosystems. Aquatic macrophytes can have a profound effect on the hydraulics and geomorphology of stream and rivers (Schoelynck et al. 2012), and within patches of vegetation flow is reduced (Vereecken et al. 2006), promoting the deposition of sediment and organic matter (Sand-Jensen 1998). This often leads to higher nutrient availability (Webster and Benfield 1986) and generally results in greater and deeper light penetration (Horppila and Nurminen 2003). However, outside a patch, faster flows can lead to the formation of erosional habitats, meaning scale-dependent feedback mechanisms may lead to self-organisation (e.g., pattern formation) of macrophyte habitat patches (Schoelynck et al. 2012). Furthermore, macrophytes provide food and habitat for invertebrates and fishes, and at intermediate biomass levels may maximize invertebrate diversity in sandy-bottomed lowland streams (Collier et al. 1999). The increased habitat complexity provided by macrophytes can reduce the effectiveness of some predators (Savino and Stein 1982), although macrophyte configuration (Crowder and Cooper 1982) and vegetation architecture of macrophytes (Warfe and Barmuta 2006) may influence rates of predation.

However, negative effects can arise in agricultural streams. For example, excessive light and nutrients, coupled with invasive macrophytes drastically altered flows leading to large-scale deposition of sediment in streams (Bunn et al. 1998). Excessive growths of macrophytes can also deplete the supply of dissolved oxygen in stream water leading to hypoxia (Caraco and Cole

2002). These negative influences further demonstrate that synergistic interactions of diffuse pollution and habitat modification can harm streams communities in modified catchments. Understanding how interactions between ecosystem engineers (e.g., macrophytes) and other consequences of land use change (e.g., increased nutrients and reduced shade) affect sediment dynamics will better enable mitigation of these problems (Jones et al. 2012).

Implications for environmental flows

In the past few decades, increased attention has been given to natural flow regimes in stream and rivers (Poff et al. 1997). In particular, one of the defining features of the natural flow regime paradigm is the appreciation of physical disturbance in shaping lotic communities, a feature lost in many regulated floodplains (Ward et al. 1999). Fluvial dynamics from flooding play a major role in maintaining habitat heterogeneity, and when floods are prevented, biodiversity may be reduced (Ward and Tockner 2001). Across the United States, the risk of biological impairment of streams doubled with increasingly diminished flows (Carlisle et al. 2010). Experimental flow reductions can decrease fluxes of deposited sediment, leading to greater sediment accumulation on the streambed and increasing ecological harm (Matthaei et al. 2010). Thus, reductions in stream water velocities, particularly during summer low-flow conditions, can lead to large volumes of sediment accumulating on the streambed (Wood and Petts 1994). Sediment deposition can be exacerbated by groundwater pumping in spring-fed streams which rely on precipitation for aquifer recharge (Wright and Berrie 1987). These studies underscore the strong nexus between flow regimes and in-stream habitat (e.g., sediment dynamics).

The effect of reduced flows and increased sediment inputs may be relevant in the spring-fed streams of lowland Canterbury where I conducted my research. Through extensive flood-

protection works (e.g., stop-banks, bunds, and tree-planting), many of these streams have lost their intermittent surface connectivity with the large braided rivers that flow eastwards from the Southern Alps. Over broad temporal scales, extreme, stochastic flooding of these rivers may have been essential to maintain and create habitat across the plains, but over a century of river regulation and agriculture on the plains has almost certainly affected sediment dynamics in many of the low-gradient streams I sampled. The causes of these changes include the removal of riparian vegetation and increased bank erosion, altering stream geomorphology through channel straightening, and by altering stream ‘assimilative capacity’ through changes to flow regimes.

These agriculture-based effects have implications for stream communities, because in New Zealand, taxa such as the ubiquitous grazing mayfly *Deleatidium*, a rheophile that is well adapted for life in unstable streams, is negatively affected by sedimentation (Ryder 1989, Dolédec et al. 1999). Towns (1987) considered that New Zealand mayflies, especially those in the dominant family Leptophlebiidae would be highly sensitive to changes to flow regimes because most species are confined to well-oxygenated, running waters. Such conditions characterise the most common river type in New Zealand: a gravel-bed river, with its run-riffle sequences and moderately straight channels (Mosley 1992). Mayfly families such as the Caenidae, which are well adapted to low-flow regimes, are not found in New Zealand, and the most diverse New Zealand family, Leptophlebiidae, has not radiated into the lentic habitats occupied by related taxa in Australia (Towns 1987); although *Deleatidium* can be found in the lotic-like shallows of wind-swept lakes (Death and Winterbourn 1995). Moreover, adaptations of many common benthic stream insects in New Zealand include high adult mobility (Townsend et al. 1997) and poorly synchronised life histories (Winterbourn 1978); characteristics that have been considered to be a response to the climatically unpredictable nature of the environment and

the short, steep catchments that characterise typical New Zealand stream and river systems (Winterbourn et al. 1981). Perhaps not surprisingly, the infilling of substrate interstices and the burial of coarse substrate by excessive sediment can have disproportionate effects on the rheophilic insects found in New Zealand that rely on this habitat to complete their life cycles (Collier and Quinn 2004). Impacts on insects with aquatic larvae and terrestrial adults may also indirectly affect the ‘permeability’ of the riparian boundary (Wiens et al. 1985, Witman et al. 2004) and the terrestrial predators that use these insects as prey subsidies (Burdon and Harding 2008).

That flow regimes can affect biotic interactions has long been recognized, and the seminal study by Wootton et al. (1996) showed how shifts in invertebrate community faunal traits in response to increased flow homogeneity could divert energy away from higher trophic levels. However, Jowett & Biggs (2009) suggested that the natural flow regime paradigm was not applicable to New Zealand, because the very flexible niches and life-history requirements of our stream organisms meant they were tolerant of a wide range of flow regimes. In my opinion, this is an overly simplistic view that ignores the importance of biotic interactions in ecosystems highly modified by multiple stressors (e.g., the effects of land-use change and invasive species). Flow regimes may not only directly (e.g., wetted-channel habitat) and indirectly (e.g., by sediment deposition) affect species’ abundances and distributions, but also influence the biotic interactions that connect communities through interactions such as herbivory, predation, and competition.

Riparian management

Mitigating the impacts of diffuse pollution is essential to creating more sustainable and environmental-friendly agriculture. In Chapter 2, degraded riparian condition contributed to in-

stream habitat quality and impacts on invertebrate communities through direct (e.g., inputs) and indirect (e.g., flow-mediated) effects on deposited sediment. The buffering effect of riparian boundaries from the impacts of agricultural land uses are well recognised (Lowrance 1998), and in particular, the role of the riparian zone in controlling non-point pollution by nutrients and sediment is universally accepted (Naiman and Decamps 1997). For example, the riparian interface can act as a sediment trap, evidenced by a North American study which found that 80-90% of sediments leaving agricultural fields in North Carolina were removed by streamside vegetation (Cooper et al. 1987). Similarly, reviews by Hill (1996) and Puckett (2002) indicated that in most circumstances more than 80% of influent nitrate was removed in riparian soils and sediments, although the weak link I found between nitrate concentrations and riparian condition in Chapter 2 was likely a feature of the Canterbury Plains, where groundwater sources of spring water strongly influence water quality.

Despite the appreciation of riparian buffers and their utility, there is still a need for knowledge regarding the optimal extent, composition and position of these buffers in the landscape to mitigate the impacts of agricultural land uses. In addition to the known benefits of riparian plantings, which include providing habitat for adult aquatic insects (Collier and Scarsbrook 2000), management practices that enhance structural complexity and food resource availability in stream ecosystems through increased detrital and prey inputs may enhance stream food webs. However, results from my research (Chapter 4) showed that there is strong potential for sediment deposition to dampen coarse detrital pathways, meaning that legacy effects of sediment may restrict the effectiveness of riparian revegetation to improving ecosystem functioning (Harding et al. 1998). Further research into how allochthonous inputs modulate

sediment impacts on stream communities and food webs is critically important in order to gain a more mechanistic understanding of ecosystem perturbation and restoration.

Despite this caveat, an increasing desire to reverse stream and river degradation by restoring key habitat characteristics and associated ecosystem processes has led to the recognition of riparian management as a means to mitigate the effects of agricultural land use on small to medium-sized streams in New Zealand (Collier et al. 2001). My results presented in Chapter 2 reinforced the need for stock exclusion through measures including riparian fencing. Unmanaged grazing is well recognized as having deleterious effects upon riparian and in-stream habitat through bank erosion and channel widening processes that can lead to altered invertebrate community composition and loss of pollution-sensitive taxa (Herbst et al. 2012). Although fencing and revegetation may help mitigate these issues, riparian plantings can also have short-term negative impacts (Davies-Colley 1997). The effects of increased shading provided by riparian plantings can cause bank erosion and increased fine sediment storage within the streambed (Quinn et al. 1997), and model forecasting has indicated that maximum sediment yields will occur approximately 15 years after planting (Collier et al. 2001). Despite this, the benefits accrued from riparian planting including shading and lower water temperatures have been predicted to lead to a 25% increase in the MCI (Macroinvertebrate Community Index; see Stark 1985); over a longer temporal scale they may outweigh the transient consequences of increased sediment loads (Collier et al. 2001) and potentially, decreased nutrient uptake (Parkyn et al. 2005).

For mitigating adverse effects, catchment modeling suggests that riparian planting should be done first in headwaters and subsequently further downstream to help to avoid nutrient yield increases, and will assist in decreasing peak loads of fine sediment (Parkyn et al. 2005). However,

sediment legacy effects may require direct human intervention to remove deposited sediment from the streambed and improve in-stream habitat (Wood and Armitage 1997, Sarriquet et al. 2007). These issues of nutrient and sediment fluxes in modified catchments reflect the need for a strong, general theory of stream ecology which addresses the role of retention and flux (e.g., ‘leakiness’) in stream and river networks (Thompson and Lake 2009), thereby helping to avoid reactive measures with short-term and small-scale benefits, but instead favouring proactive actions incorporating long-term planning that ensure greater resilience for impending problems (Palmer et al. 2008).

Climate change and sediment dynamics

The predicted global climate change (IPCC 2001) is expected to exert stress on lotic communities (Carpenter et al. 1992, Woodward et al. 2010) through direct (Hogg and Williams 1996, Xenopoulos et al. 2005) and indirect pathways (Scheurer et al. 2009, Heathwaite 2010). An indirect pathway may be manifested through increased sediment inputs due to altered vegetation composition (Stromberg et al. 2010), forest fires (Beaty 1994, Minshall et al. 2001), permafrost degradation and glacial recession (Lu et al. 2010), in combination with fluctuating rainfall patterns and more frequent extreme weather events (IPCC 2001). However, although increased sediment flux and retention is likely to be a significant corollary of climate change, it has been largely overlooked in the recent literature investigating the potential consequences for freshwater ecosystems (Woodward et al. 2010). Heathwaite (2010) suggests that the reductionist approaches which have focused on direct effects such as increased water temperatures are unable to provide the overall concepts or methods to understand how system properties will emerge in response to a changing climate.

Moreover, in regions dominated by agriculture, the changing spatial and temporal distribution of precipitation (Milly et al. 2005) coupled with increased demand for water resources (Jackson et al. 2001) and the intensity of farming practices (Tilman et al. 2001) could have synergistic effects on anthropogenic stressors in freshwaters (Heathwaite 2010). The effects of flow on sediment dynamics have been discussed previously, but predicting the effect of increased abstraction for irrigation with increased climate uncertainty requires researching the minimum flows required to maintain suitable habitat for fauna sensitive to deposited sediment (Milhous 1998). Likewise, managing soil conservation is of the utmost importance, because the loss of soil carbon from agricultural lands through poor land management practices may have unintended consequences by creating a source of carbon emissions entering the atmosphere (Lal 2004). As an example, methane production from a southern English chalk stream was associated with increased sedimentation and the influence of extensive macrophyte growths, thus indicating another negative consequence of agriculture (Sanders et al. 2007).

CONCLUDING REMARKS

My thesis has shown that sedimentation influences streams at multiple levels of biological organisation (i.e., communities, food webs, and ecosystems). I found strong evidence to suggest that sediment deposition increased environmental stress by making suitable habitats and associated food resources less available (e.g., cobbles with associated periphyton and leaves), and potentially increasing substrate instability, thus contributing to changes at the community level. These changes were predicted to influence higher levels of biological organisation (food webs and ecosystem processes; Chapter 1). Although I found evidence that sediment-induced change to resource availability generated non-linear responses (i.e., thresholds) by invertebrate communities (Chapter 2), I did not observe similar thresholds in other stream responses.

However, sediment was associated with functional changes in stream ecosystems that included shifts in invertebrate-feeding traits from more specialised ‘grazers’ and ‘shredders’ to generalist ‘collectors’ and ‘deposit-feeders’. These changes, coupled with shifts in basal resource quality and availability appeared to contribute to a ‘compression’ of trophic niche space, thus leading to simpler food webs (Chapter 3). Sedimentation appeared to alter invertebrate functional diversity and consumer niche partitioning, thus impairing ecosystem function, as demonstrated by a reduction in litter breakdown rates (Chapter 4). My thesis research has helped to identify potential sediment influences on streams and rivers across multiple levels of biological organisation, thus helping to better understand the ecological consequences of this pervasive problem. Moreover, by identifying potential sediment thresholds, river and stream management will be enhanced. Establishing a strong theoretical basis, coupled with observational and experimental approaches is fundamental to better understanding the impacts of sediment as a ‘universal stressor’ of freshwaters. This knowledge is crucial if we are to preserve biodiversity and ecosystem function in streams, rivers, and their receiving environments (e.g., lakes and coastal waters) affected by human land uses.

LITERATURE CITED

- Anderson, C., and G. Cabana. 2009. Anthropogenic alterations of lotic food web structure: evidence from the use of nitrogen isotopes. *Oikos* 118:1929-1939.
- Anlauf, K. J., and C. M. Moffitt. 2010. Modelling of landscape variables at multiple extents to predict fine sediments and suitable habitat for *Tubifex tubifex* in a stream system. *Freshwater Biology* 55:794-805.
- Beaty, K. G. 1994. Sediment transport in a small stream following 2 successive forest-fires. *Canadian Journal of Fisheries and Aquatic Sciences* 51:2723-2733.

- Beisel, J. N., P. Usseglio-Polatera, and J. C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422:163-171.
- Benoy, G. A., A. B. Sutherland, J. M. Culp, and R. B. Brua. 2012. Physical and ecological thresholds for deposited sediments in streams in agricultural landscapes. *Journal of Environmental Quality* 41:31-40.
- Bond, N. R., and B. J. Downes. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* 48:455-465.
- Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6:316-325.
- Bryce, S. A., G. A. Lomnický, and P. R. Kaufmann. 2010. Protecting sediment sensitive aquatic species in mountain streams through the application of biologically based criteria streambed sediment criteria. *Journal of the North American Benthological Society* 29:657–672.
- Bunn, S. E., P. M. Davies, D. M. Kellaway, and I. P. Prosser. 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* 39:171-178.
- Burdon, F. J., and J. S. Harding. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology* 53:330-346.
- Burdon, F. J., A. R. McIntosh, and J. S. Harding. *in press*. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. *Ecological Applications* doi:10.1890/12-1190.1.

- Cairns, J., Jr. 1977. Aquatic ecosystem assimilative capacity. *Fisheries* 2:5-7.
- Caraco, N. F., and J. J. Cole. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecological Applications* 12:1496-1509.
- Carlisle, D. M., and W. H. Clements. 2005. Leaf litter breakdown, microbial respiration and shredder production in metal-polluted streams. *Freshwater Biology* 50:380-390.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2010. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264–270.
- Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23:119-139.
- Collier, K. J., P. D. Champion, and G. F. Croker. 1999. Patch- and reach-scale dynamics of a macrophyte-invertebrate system in a New Zealand lowland stream. *Hydrobiologia* 392:89-97.
- Collier, K. J., and J. M. Quinn. 2004. Factors affecting distribution and abundance of the mayfly *Acanthophlebia cruentata* (Leptophlebiidae) in North Island, New Zealand, streams. *New Zealand Entomologist* 27:17-28.
- Collier, K. J., J. C. Rutherford, J. M. Quinn, and R. J. Davies-Colley. 2001. Forecasting rehabilitation outcomes for degraded New Zealand pastoral streams. *Water Science and Technology* 43:175-184.
- Collier, K. J., and M. K. Scarsbrook 2000. Use of riparian and hyporheic habitats. Pgs 179-206 in *New Zealand stream invertebrates: ecology and implications for management*. K. J. Collier and M. J. Winterbourn (eds.). New Zealand Limnological Society, Christchurch, NZ.

- Cooper, J. R., J. W. Gilliam, R. B. Daniels, and W. P. Robarge. 1987. Riparian areas as filters for agricultural sediment. *Soil Science Society of America Journal* 51:416-420.
- Costantini, M. L., and L. Rossi. 2010. Species diversity and decomposition in laboratory aquatic systems: the role of species interactions. *Freshwater Biology* 55:2281-2295.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802-1813.
- Culp, J. M., S. J. Walde, and R. W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1568-1574.
- Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64:1345-1351.
- Davies-Colley, R. J. 1997. Stream channels are narrower in pasture than in forest. *New Zealand Journal of Marine and Freshwater Research* 31:599.
- Death, R. G. 2000. Invertebrate-substratum relationships. Pgs 157-178 *in* New Zealand stream invertebrates: ecology and implications for management. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Death, R. G. 2010. Disturbance and riverine benthic communities: What has it contributed to general ecological theory? *River Research and Applications* 26:15-25.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76:1446-1460.
- Dolédec, S., B. Statzner, and M. Bournard. 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology* 42:737-758.

- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487-515.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52:483-498.
- Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology & Evolution* 25:372-380.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95:14843-14847.
- Harrison, S. S. C., J. L. Pretty, D. Shepherd, A. G. Hildrew, C. Smith, and R. D. Hey. 2004. The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology* 41:1140-1154.
- Harvey, G. L., T. P. Moorhouse, N. J. Clifford, A. J. Henshaw, M. F. Johnson, D. W. Macdonald, I. Reid, and S. P. Rice. 2011. Evaluating the role of invasive aquatic species as drivers of fine sediment-related river management problems: The case of the signal crayfish (*Pacifastacus leniusculus*). *Progress in Physical Geography* 35:517-533.
- Heathwaite, A. L. 2010. Multiple stressors on water availability at global to catchment scales: understanding human impact on nutrient cycles to protect water quality and water availability in the long term. *Freshwater Biology* 55:241-257.

- Herbst, D. B., M. T. Bogan, S. K. Roll, and H. D. Safford. 2012. Effects of livestock exclusion on in-stream habitat and benthic invertebrate assemblages in montane streams. *Freshwater Biology* 57:204-217.
- Hill, A. R. 1996. Nitrate removal in stream riparian zones. *Journal of Environmental Quality* 25:743-755.
- Hogg, I. D., and D. D. Williams. 1996. Response of stream invertebrates to a global-warming thermal regime: An ecosystem-level manipulation. *Ecology* 77:395-407.
- Holomuzki, J. R., J. W. Feminella, and M. E. Power. 2010. Biotic interactions in freshwater benthic habitats. *Journal of the North American Benthological Society* 29:220-244.
- Homan, R. N., B. S. Windmiller, and J. M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14:1547-1553.
- Horppila, J., and L. Nurminen. 2003. Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). *Water Research* 37:4468-4474.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, USA.
- Hubbell, S. P., and J. K. Lake 2002. The neutral theory of biodiversity and biogeography, and beyond. Pgs 45-63 *in* *Macroecology: concepts and consequences*. T. M. Blackburn and K. J. Gaston (eds.). Blackwell Publishing, Oxford, UK.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.

- IPCC. 2001. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK.
- Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. *Ecology* 11:1027-1045.
- Jennings, S., J. K. Pinnegar, N. V. C. Polunin, and T. W. Boon. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology* 70:934-944.
- Jessup, B. K., D. Eib, L. Guevara, J. Hogan, F. John, S. Joseph, P. Kaufmann, and A. Kosfiszer. 2010. Sediment in New Mexico streams: existing conditions and potential benchmarks. Report prepared for the U.S. Environmental Protection Agency, Region 6, Dallas, TX and the New Mexico Environment Department, Santa Fe, NM. Prepared by Tetra Tech, Inc., Montpelier, VT, USA.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946-1957.
- Jones, J. I., A. L. Collins, P. S. Naden, and D. A. Sear. 2012. The relationship between fine sediment and macrophytes in rivers. *River Research and Applications* 28:1006-1018.
- Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28:1055-1071.
- Jones, R. I., and J. Grey. 2011. Biogenic methane in freshwater food webs. *Freshwater Biology* 56:213-229.

- Jowett, I. G., and B. J. F. Biggs. 2009. Application of the 'natural flow paradigm' in a New Zealand context. *River Research and Applications* 25:1126-1135.
- Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304:1623-1627.
- Larsen, S., I. P. Vaughan, and S. J. Ormerod. 2009. Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biology* 54:203-219.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467-494.
- Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399-1410.
- Lenat, D. R., D. L. Penrose, and K. W. Eagleson. 1979. Biological evaluation of non-point source pollutants in North Carolina streams and rivers. Biological Series 102. North Carolina Department of Natural Resources and Community Development, Raleigh, North Carolina, USA.
- Lowrance, R. 1998. Riparian forest ecosystems as filters for nonpoint-source pollution. Pgs 113-141 *in* Successes, limitations, and frontiers in ecosystem science. M. L. Pace and P. M. Groffman (eds.). Springer-Verlag, New York, USA.
- Lu, X., S. Zhang, and J. Xu. 2010. Climate change and sediment flux from the Roof of the World. *Earth Surface Processes and Landforms* 35:732-735.
- Matthaei, C. D., J. J. Piggott, and C. R. Townsend. 2010. Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology* 47:639-649.

- McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65:894-908.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794-798.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature* 422:881-885.
- McTammany, M. E., E. F. Benfield, and J. R. Webster. 2008. Effects of agriculture on wood breakdown and microbial biofilm respiration in southern Appalachian streams. *Freshwater Biology* 53:842-854.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21-54.
- Milhous, R. T. 1998. Modelling of instream flow needs: the link between sediment and aquatic habitat. *River Research and Applications* 14:79-94.
- Milly, P. C. D., K. A. Dunne, and A. V. Vecchia. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature* 438:347-350.
- Minshall, G. F., J. T. Brock, D. A. Andrews, and C. T. Robinson. 2001. Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* 10:185-199.
- Molinos, J. G., and I. Donohue. 2009. Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society* 28:110-121.
- Mosley, M. P. 1992. River morphology. Pgs 285-304 *in* Waters of New Zealand. M. P. Mosley (eds.). New Zealand Hydrological Society, Wellington, NZ.

- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Navel, S., F. Mermillod-Blondin, B. Montuelle, E. Chauvet, L. Simon, C. Piscart, and P. Marmonier. 2010. Interactions between fauna and sediment control the breakdown of plant matter in river sediments. *Freshwater Biology* 55:753-766.
- Newman, M. 2011. Molecular phylogenetic characterization of microbial community dynamics associated with freshwater stream environmental organic matter sources. Ph.D thesis. Department of Biological Sciences, University of Auburn, Alabama, USA.
- Nuttall, P. M., and G. H. Bielby. 1973. The effect of china-clay wastes on stream invertebrates. *Environmental Pollution* 5:77-86.
- O'Gorman, E. J., and M. C. Emmerson. 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences* 106:13393-13398.
- Palmer, M. A., C. A. R. Liermann, C. Nilsson, M. Florke, J. Alcamo, P. S. Lake, and N. Bond. 2008. Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and the Environment* 6:81-89.
- Pardini, R., A. d. A. Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE* 5:e13666.
- Parkyn, S. M., R. J. Davies-Colley, A. B. Cooper, and M. J. Stroud. 2005. Predictions of stream nutrient and sediment yield changes following restoration of forested riparian buffers. *Ecological Engineering* 24:551-558.

- Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of community structure. Pgs 303-324 *in* Dynamics of Lotic Ecosystems. T. D. Fontaine and S. M. Bartell (eds.). Ann Arbor Science Publishers Ann Arbor, MI, USA.
- Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* 64:393-418.
- Poff, L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. *BioScience* 47:769-784.
- Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems - Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.
- Post, D. M., and G. Takimoto. 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116:775-782.
- Puckett, L. J. 2002. Hydrogeologic controls on the transport and fate of nitrate in ground water beneath riparian buffer zones: results from thirteen studies across the United States. *Water Science and Technology* 49:47-53.
- Quinn, J. M., A. B. Cooper, R. J. Davies-Colley, J. C. Rutherford, and R. B. Williamson. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill country streams. *New Zealand Journal of Marine and Freshwater Research* 31:579-597.

- Relyea, C. D., G. W. Minshall, and R. J. Danehy 2000. Stream insects as bioindicators of fine sediment. Pgs 663-686 in *Proceedings of the Water Environment Federation Watershed Management 2000 Conference*. (eds.). Water Environment Federation, Alexandria, VA, USA.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265-269.
- Rosenberg, D. M., and A. P. Wiens. 1978. Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river. *Water Research* 12:753-763.
- Rounick, J. S., and M. J. Winterbourn. 1983. Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. *Archiv für Hydrobiologie* 96:448-474.
- Ryder, G. I. 1989. Experimental studies on the effects of fine sediments on lotic invertebrates. Ph.D. thesis. Department of Zoology, University of Otago, Dunedin, NZ.
- Sand-Jensen, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology* 39:663-679.
- Sanders, I. A., C. M. Heppell, J. A. Cotton, G. Wharton, A. G. Hildrew, E. J. Flowers, and M. Trimmer. 2007. Emission of methane from chalk streams has potential implications for agricultural practices. *Freshwater Biology* 52:1176-1186.
- Sarriquet, P. E., P. Bordenave, and P. Marmonier. 2007. Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River Research and Applications* 23:815-828.

- Savino, J. F., and R. A. Stein. 1982 Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. . Transactions of the American Fisheries Society 111:255-266.
- Scheurer, K., C. Alewell, D. Banninger, and P. Burkhardt-Holm. 2009. Climate and land-use changes affecting river sediment and brown trout in alpine countries: a review. Environmental Science and Pollution Research 16:232-242.
- Schoelynck, J., T. de Groote, K. Bal, W. Vandenbruwaene, P. Meire, and S. Temmerman. 2012. Self-organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation. Ecography 35:760-768.
- Scrimgeour, G. J., and M. J. Winterbourn. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. Hydrobiologia 171:33-44.
- Stark, J. D. 1985. A macroinvertebrate community index of water quality for stony streams. Water & Soil Miscellaneous Publication No. 87. National Water and Soil Conservation Authority, Wellington, NZ.
- Statzner, B. 2012. Geomorphological implications of engineering bed sediments by lotic animals. Geomorphology 157–158:49-65.
- Stromberg, J. C., S. J. Lite, and M. D. Dixon. 2010. Effects of stream flow patterns on riparian vegetation of a semiarid river: Implications for a changing climate. River Research and Applications 26:712-729.
- Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969-974.

- Thompson, R. M., and S. P. Lake. 2009. Reconciling theory and practise: The role of stream ecology. *River Research and Applications* 26:5-14.
- Thompson, R. M., and C. Townsend. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75:476-484.
- Thomson, J. R., P. S. Lake, and B. J. Downes. 2002. The effect of hydrological disturbance on the impact of a benthic invertebrate predator. *Ecology* 83:628-642.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.
- Tonkin, J. D., and R. G. Death. 2012. Consistent effects of productivity and disturbance on diversity between landscapes. *Ecosphere* 3:art108.
- Towns, D. R. 1987. The mayflies (Ephemeroptera) of Great Barrier Island, New Zealand: macro- and micro-distributional comparisons. *Journal of the Royal Society of New Zealand* 17:349-361.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society* 16:531-544.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A.-M. Klein, N. Buchmann, J. Perner, and T. Tscharncke. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol* 6:e122.

- Vasconcelos, M. D., and A. S. Melo. 2008. An experimental test of the effects of inorganic sediment addition on benthic macroinvertebrates of a subtropical stream. *Hydrobiologia* 610:321-329.
- Vereecken, H., J. Baetens, P. Viaene, F. Mostaert, and P. Meire. 2006. Ecological management of aquatic plants: effects in lowland streams. *Hydrobiologia* 570:205-210.
- Wagenhoff, A., C. R. Townsend, and C. D. Matthaei. 2012. Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology* 49:892-902.
- Walters, A. W., and D. M. Post. 2008. An experimental disturbance alters fish size structure but not food chain length in streams. *Ecology* 89:3261-3267.
- Ward, J. V., and K. Tockner. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* 46:807-819.
- Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* 15:125-139.
- Warfe, D., and L. Barmuta. 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia* 150:141-154.
- Waters, T. F. 1982. Annual production by a stream brook charr population and by its principal invertebrate food. *Environmental Biology of Fishes* 7:165-170.
- Waters, T. F. 1995. Sediment in streams. sources, biological effects, and control. American Fisheries Society, Bethesda, Maryland, USA.
- Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.

- White, J. L., and B. C. Harvey. 2001. Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. *Freshwater Biology* 46:987-995.
- Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
- Winterbourn, M. J. 1978. The macroinvertebrate fauna of a New Zealand forest stream. *New Zealand Journal of Marine and Freshwater Research* 5:157-169.
- Winterbourn, M. J. 2000. Feeding ecology. Pgs 100-124 *in* New Zealand stream invertebrates: ecology and implications for management. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15:321-328.
- Witman, J. D., J. C. Ellis, and W. B. Anderson 2004. The influence of physical processes, organisms, and permeability on cross-ecosystem fluxes. Pgs 335-358 *in* Food webs at the landscape level. G. A. Polis, M. E. Power and G. R. Huxel (eds.). The University of Chicago Press, Chicago, Illinois, USA.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21:203-217.
- Wood, P. J., and G. E. Petts. 1994. Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management* 9:303-316.
- Woodward, G. 2009. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology* 54:2171-2187.

- Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2093-2106.
- Woodward, G. U. Y., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. *Freshwater Biology* 47:777-798.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558-1561.
- Wright, J. F., and A. D. Berrie. 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management* 1:145-160.
- Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience* 56:203-209.
- Xenopoulos, M. A., D. M. Lodge, J. Alcamo, M. Märker, K. Schulze, and D. P. V. Vuuren. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology* 11:1557-1564.
- Yule, C. M., L. Boyero, and R. Marchant. 2010. Effects of sediment pollution on food webs in a tropical river (Borneo, Indonesia). *Marine and Freshwater Research* 61:204-213.

APPENDICES

CHAPTER 2

APPENDIX A. Map and table describing site locations and basic physico-chemical parameters.

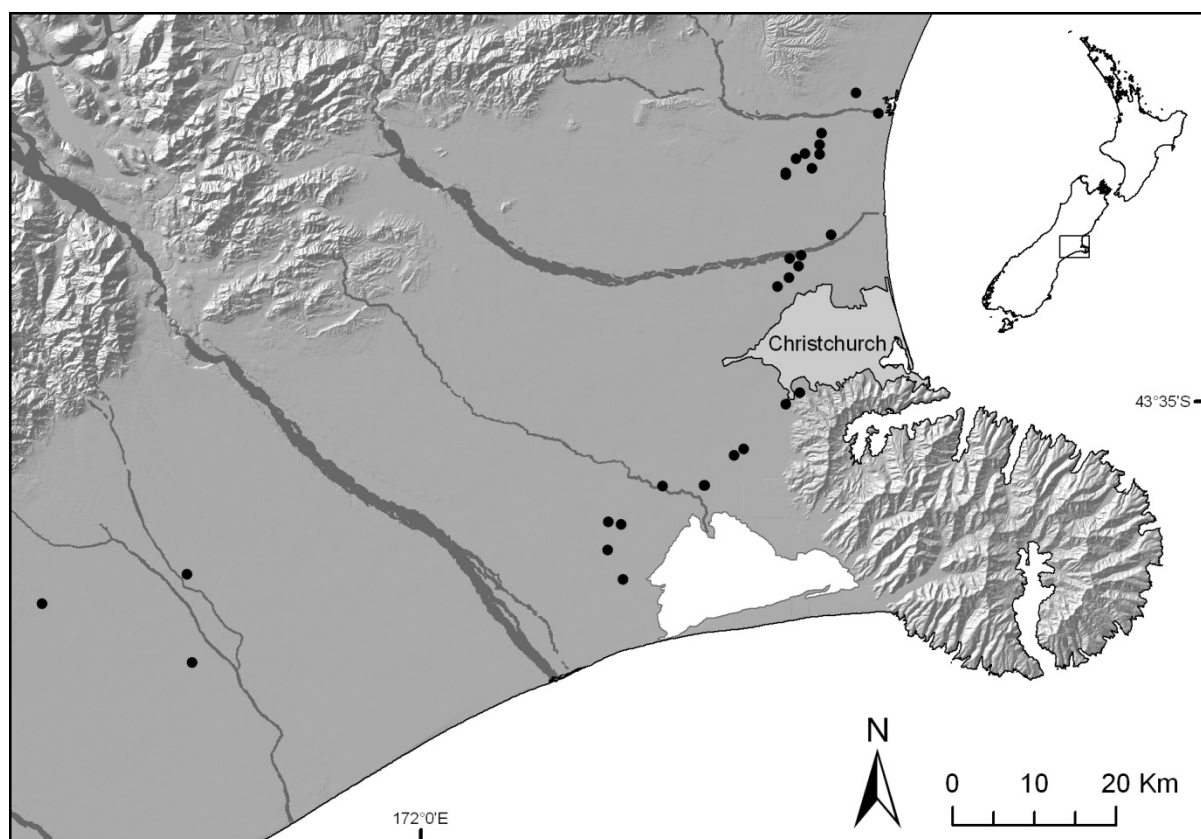


FIG. 1. The 30 survey streams (black circles) sampled along gradients of deposited sediment and dissolved nutrients located on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010.

TABLE 1. Physico-chemical characteristics of 30 streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. Fine sediment cover was assessed at two different spatial scales; only reach-scale (30 m) data is presented here. Lat., latitude; Long., longitude; SC, specific conductivity ($\mu\text{S}_{25^\circ \text{C}}/\text{cm}$); Nitrate, nitrate-nitrite (mg/L); DRP, dissolved reactive phosphorus ($\mu\text{g/L}$); DO, dissolved oxygen (mg/L); Temp., temperature ($^\circ\text{C}$); Width, wetted stream width (m); % Fines, fine sediment (% cover reach); SIS, suspendable inorganic sediment (g/m^2).

Site	Stream	Lat. ($^\circ\text{N}$)	Long. ($^\circ\text{S}$)	pH	SC	Nitrate	DRP	DO	Temp.	Width	% Fines	SIS
1.	Waimakariri Trib.	-43.439	172.568	7.87	70	0.15	8.4	10.4	12.9	1.53	2.5	11
2.	Springston South I	-43.687	172.436	7.44	290	5.46	10.9	10.2	13.3	2.15	10.3	225
3.	Hinds Creek	-43.808	171.429	7.17	146	4.36	10.9	10.0	11.5	3.70	0.8	12
4.	Springston South II	-43.688	172.437	7.34	323	7.12	7.8	8.97	12.1	2.20	39.7	290
5.	Plasketts Drain	-43.345	172.563	7.60	151	2.96	24.2	9.48	12.2	2.60	3.6	57
6.	Easterbrook	-43.329	172.578	7.93	138	2.83	15.7	8.87	14.7	3.50	89.9	892
7.	Shipleys Creek	-43.459	172.566	7.52	71	0.19	6.3	9.77	13.1	5.40	76.1	814
8.	Springs Creek	-43.655	172.482	7.60	106	1.82	11.7	8.58	12.8	3.97	100.0	355
9.	Southbrook	-43.323	172.592	7.20	115	1.40	11.6	9.47	12.8	2.80	4.2	12
10.	Flaxton Drain	-43.340	172.602	7.97	146	1.72	18.0	11.3	17.3	2.53	42.2	175
11.	Hobbs Creek	-43.648	172.496	7.45	229	5.66	13.2	7.76	14.0	3.30	89.7	1243
12.	Waihikuawa	-43.435	172.585	7.49	71	0.03	6.7	8.42	12.4	3.15	19.4	244
13.	Boggy Creek	-43.727	172.290	7.57	257	8.65	9.3	8.32	15.7	3.40	5.8	63
14.	McGees Creek	-43.730	172.309	7.30	269	7.22	14.0	5.65	16.1	1.90	36.9	155
15.	Leeston-Dunsandel	-43.757	172.289	7.85	103	1.20	3.8	8.70	15.4	1.98	85.0	740

TABLE 1. Continued.

Site	Stream	Lat. (°N)	Long. (°S)	pH	SC	Nitrate	DRP	DO	Temp.	Width	% Fines	SIS
16.	Cridges Creek	-43.469	172.549	7.17	74	0.04	36.1	7.78	15.0	4.27	7.5	45
17.	Middle Brook	-43.324	172.613	7.20	116	0.62	13.6	10.7	15.5	2.07	48.3	1350
18.	Northbrook	-43.314	172.613	6.95	97	0.36	2.6	10.9	14.3	3.20	18.1	392
19.	Saltwater Creek	-43.257	172.669	7.96	102	0.18	10.8	11.3	13.2	3.58	20.8	534
20.	Waikuku Creek	-43.280	172.702	7.05	112	0.51	28.2	11.0	15.7	2.92	29.7	1050
21.	Cashmere Stream	-43.586	172.582	7.28	216	1.74	2.6	10.7	13.8	1.82	98.1	2351
22.	Halswell River	-43.599	172.561	7.64	240	5.96	125.8	10.5	14.4	4.63	96.0	17800
23.	Clearwater	-43.447	172.581	7.65	64	0.44	2.9	12.7	15.2	3.35	13.1	151
24.	Coldstream	-43.301	172.616	6.81	103	0.12	13.5	11.3	13.8	2.27	19.4	278
25.	Shearers Stream	-43.778	171.650	7.77	127	3.10	12.2	10.6	13.9	5.31	15.3	107
26.	Timaru-Track Rd	-43.875	171.656	7.62	250	8.79	5.3	9.26	12.6	1.48	99.2	7449
27.	Cust River	-43.346	172.563	7.12	182	5.38	11.8	12.1	14.4	5.92	0.6	48
28.	Birdlings Brook	-43.790	172.312	7.21	241	6.11	5.1	9.45	12.8	2.37	10.8	317
29.	Courtenay Stream	-43.413	172.630	6.92	185	5.39	9.5	7.82	14.3	2.97	83.3	4480
30.	Selwyn River	-43.688	172.373	7.34	212	5.69	6.7	8.95	15.0	5.92	1.1	42

APPENDIX B. Detailed descriptions of specific variables and statistical methods used in analyses.

B.1 Explanation of nitrate as principal nutrient variable used in analyzes.

Because samples had minimal nitrite concentrations close to detection limits (< 5%), nitrite-nitrate nitrogen concentrations have been reported as nitrate. Previous research (Greenwood et al. 2007) on streams in our region found that nutrient concentrations including ammonia (NH_4^+) were well below the levels toxic to invertebrates, and specific conductivity was the strongest predictor of invertebrate community composition (~ % EPT), thus suggesting that nitrate, which is strongly correlated to this variable in our region, is the most appropriate measure of dissolved nitrogen to use.

B.2 Detailed description of partial redundancy analyzes testing effects of sediment, nitrate and site location on invertebrate community composition.

B.2.1 Data transformations

Partial redundancy analysis (*p*RDA) simultaneously quantified the amount of variability in community composition that could be attributed to sediment, nitrate, and spatial factors independently, whilst also assessing the joint covariance between these variables. Prior to analyzes, the invertebrate community data were Hellinger-transformed, as suggested by Legendre and Gallagher (2001), to allow the use of Euclidean-based ordination methods (i.e., *p*RDA). Hellinger-transformations also offer the advantage of not strongly weighting rare taxa in the analyzes (Legendre and Gallagher 2001).

B.2.2 Spatial data

Space was represented by a matrix generated using Principal Coordinates of Neighbors Matrices (PCNM) analysis. PCNM is a method for detecting and quantifying spatial patterns over a range of difference scales. Latitude and longitude were first converted into Cartesian coordinates (X, Y). Using the X and Y coordinates; a matrix of PCNM variables was created using the “pcnm” command in R. The default truncation distance was used; this is the longest distance to keep data connected (Borcard and Legendre 2002). This analysis yielded 6 PCNM variables.

B.2.3 Display of results

The results of the *p*RDA analyzes were displayed in area-proportional Venn diagrams using ellipses, where the area of the ellipse represented the proportion of variance (positive and negative) explained by each factor. These diagrams were drawn using the eulerAPE program (Version 2.0.3, School of Computing, University of Kent, UK).

B.3 Detailed description of change-point analyzes identifying sediment thresholds.

Change-point analysis (CPA) uses a combination of cumulative sum (CUSUM) and bootstrapping methods. The CUSUM is calculated as:

$$C_s = \sum_{i=1}^s (x_i - \bar{x})$$

where C_s is the cumulative sum value at sediment variable s (ordered from lowest to highest) of the invertebrate variable x_i (i.e. % EPT) and \bar{x} is the series mean. Changes in the direction and/or slope of the CUSUM plot are indicative of shifts in the data trend or a change in the local average

of the series. To detect these changes objectively, 10,000 ‘bootstrapping’ procedures were performed by re-sampling the original series without replacement (i.e. re-orders the entire data set by random selection of data points). This allows the generation of bootstrapped CUSUM curves, which are then compared statistically with the original CUSUM plot (Taylor 2000). The difference d between the maximum and minimum CUSUM values of each bootstrap is then compared with the original data’s d , and from this comparison the confidence of change in the series can be determined (Taylor 2000). Only break-points with a probability of change >99% and 95% confidence intervals were considered.

B.4 Detailed description of reach chlorophyll- a index used in the sediment structural equation model.

The reach index of chlorophyll- a was calculated by multiplying the chlorophyll- a concentrations (mg/cm^2) from cobbles and fine sediment by the proportional cover of these substrate types within each respective study reach, whilst correcting for differences in rugosity (complexity). This correction factor used the ratio of variance in rugosity of cobbles (rocks) and fine sediment (sand) as measured by Shumway et al. (2007) to allow for differences in substrate complexity.

B.5 Detailed description of goodness of fit measures used for structural equation models.

The chi-square (χ^2) test of model fit was used to determine whether the fit between the structural equation model (SEM) and data was satisfactory ($P > 0.05$), since a non-significant result is a strong indication of an adequate fit (Grace 2006). The standardized root mean square residual (SRMR) is the standardized square root of the difference between the residuals of the sample covariance matrix and hypothesized covariance model. Values range from 1 to 0, where well-

fitted models obtain values < 0.05 (Hu and Bentler 1999). The incremental fit index (IFI) is a relative fit index which compares a chi-square for the model tested to one from a null model (also known as the 'baseline' or 'independence' model), and the resulting value ranges from 0 to 1, where values greater than 0.95 indicate a good fitting model (Hu and Bentler 1999). The IFI was chosen over the root mean square error of approximation (RMSEA), which tends to over-reject true population models when sample sizes are low (Hu and Bentler 1999). In contrast, the IFI is independent of sample size (Bollen 1990).

LITERATURE CITED

- Bollen, K. A. 1990. Overall fit in covariance structure models: Two types of sample size effects. *Psychological Bulletin* 107:256-259.
- Borcard, D. and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153:51-68.
- Grace, J. B. 2006. *Structural Equation Modeling and Natural Systems*. Cambridge University Press Cambridge, UK.
- Greenwood, M. J., J. S. Harding, D. K. Niyogi, and A. R. McIntosh. 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology* 49:213-222.
- Hu, L. and P. M. Bentler. 1999. Cutoff criteria for fit indexes in covariance structure analysis: Coventional criteria versus new alternatives. *Structural Equation Modeling* 6:1-55.
- Legendre, P. and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271-280.

Shumway, C. A., H. A. Hofmann, and A. P. Dobberfuhl. 2007. Quantifying habitat complexity in aquatic ecosystems. *Freshwater Biology* 52:1065-1076.

Taylor, W. A. 2000. Change-point analysis: a powerful new tool for detecting changes. Available from: <http://www.variation.com/cpa/tech/changepoint.html> (Date accessed: 6-5-2012).

APPENDIX C. Variables used to calculate a subjective index of riparian condition.

TABLE C1. Subjective scores for riparian attributes used to calculate an index of riparian condition (from Harding et al. 2009).

Attributes	L	R	Scores 1	Scores 2	Scores 3	Scores 4	Scores 5
Shading of water			Little or no shading	10-25% shading	25-50%	50-80%	>80%
Buffer width			<1 m	1-5 m	5-15 m	15-30 m	>30 m
Buffer intactness			Buffer absent	50-99% gaps	20-50% gaps	1-20% gaps	Completely intact
Vegetation comp. of buffer and/or adjacent land to 30 m from streambank	Buffer		Short grazed pasture grasses to stream edge, or impervious surfaces	Exotic weedy shrubs Gorse, blackberry, broom, or mainly high grasses or low native shrubs 0.3-2 m	Deciduous tree dominated; native shrub dom. (2-5 m); or plantation with <25% cover of >5 m trees; or tussock where natural	Regenerating native forest or woodlot evergreens with >25% cover sub-canopy (>5 m) trees but <10% canopy trees (>12 m)	Maturing native forest including >10% cover canopy trees (>12 m); or native wetland or natural tussock veg.
	Adjacent land						
Bank stability			Very low: uncohesive sediments & few roots & >40% recently eroded	Low: uncohesive sediments & few roots/low veg. cover & >15-40% recently eroded	Moderate: stabilized by geology (e.g. cobbles), veg cover &/or roots & >5-15% recently eroded	High: stabilized by geology (e.g. bedrock), veg. cover &/or roots; & 1-5% recently eroded	Very high: stabilized by geology (e.g. bedrock), veg. cover &/or roots; <1% recently eroded
Livestock access			High: unfenced and unmanaged with active livestock use	Moderate: some livestock access	Limited: unfenced but low stocking, bridges, troughs, natural deterrents	Very limited: temporary fencing of all livestock or naturally very limited access	None: permanent fencing or no livestock
Riparian soil denitrification potential			Soils dry/firm underfoot or moist-wet but frequent tile drains bypass riparian soils (≥ 3 per 100 m)	1-30% streambank soils moist but firm or moist-wet with infrequent bypass drains (1-2 per 100 m)	$\geq 30\%$ streambank soils moist but firm underfoot. No drains.	1-30% streambank soils water-logged, soft underfoot with black soil. No drains.	$\geq 30\%$ of streambanks water-logged, surface moist/fluid underfoot. No drains.
Land slope 0-30 m from stream bank			>35°	>20-35°	>10-20°	>5-10°	0-5°
Groundcover of buffer and/or adjacent land to 30 m from streambank	Buffer						
	Adjacent land		Bare	Short/regularly grazed pasture (<3 cm)	Pasture grass/tussock with bare flow paths or 2-3 cm tree litter layer	Moderate density grass or dense (>3 cm) tree litter layer	High density long grass
Soil drainage			Impervious (e.g. sealed) or extensively pugged and/or compacted soil	Low permeability (e.g. high clay content) or moderately pugged/compacted soil	Low-moderate permeability (e.g. silt/loam) and not pugged/compacted	Mod-high permeability (e.g. sandy loam) & not pugged/compacted	Very high permeability (e.g. pumice/sand) & not pugged/compacted
Rills/channels			Frequent rills (> 9 per 100 m) or larger channels carry most runoff	Common rills (4-9 per 100 m) or 1-2 larger channels carry some runoff	Infrequent rills (2-3 per 100 m) and no larger channels	Rare rills (1 per 100 m) and no larger channels	None

LITERATURE CITED

Harding, J. S., J. Clapcott, J. Quinn, J. Hayes, M. Joy, R. Storey, H. Greig, J. Hay, T. James, M.

Beech, R. Ozane, A. Meredith, and I. Boothroyd. 2009. Stream habitat assessment protocols

for wadeable rivers and streams of New Zealand. School of Biological Sciences, University of

Canterbury Christchurch, New Zealand.

APPENDIX D. Results from principal component analyzes used to reduce variables.

TABLE 1. Results from principal component analyzes (PCA) used to reduce selected physical and biological variables. SIS, suspendable inorganic sediment; SFPM, suspended fine-particulate matter; DFPM, deposited fine-particulate matter. See Appendix H for a detailed description of the chlorophyll-*a* index.

PCA Model		PCA Axis 1	PCA Axis 2
Sediment	% Variation	89.0	8.1
	<i>Eigenvectors</i>		
	% Sediment cover (reach)	-0.52	0.31
	% Sediment cover (patch)	-0.50	0.58
	log SIS (g/m ²)	-0.48	-0.73
	log Sediment depth (mm)	-0.51	-0.20
Habitat availability	% Variation	77.7	13.4
	<i>Eigenvectors</i>		
	Embeddedness	-0.41	0.09
	Substrate size (cm)	-0.41	-0.02
	Sorting index (SI)	-0.38	-0.12
	% Pebbles cover (patch)	-0.31	0.66
	% Cobbles cover (patch)	-0.38	-0.43
	% Pebbles cover (reach)	-0.38	0.38
	% Cobbles cover (reach)	-0.37	-0.47
Food availability	% Variation	54.5	19.2
	<i>Eigenvectors</i>		
	% Organics (Periphyton/biofilm)	-0.53	-0.14
	% Organics (SFPM)	-0.53	0.31
	% Organics (DFPM)	-0.49	0.52
	Chlorophyll- <i>a</i> index	-0.44	-0.79

APPENDIX E. Invertebrate community abundance data and results of partial redundancy analysis.

TABLE 1. Invertebrate community abundance data (mean individuals/0.0625 m²) from streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010.

PART A: Sites 1-15. See Appendix A (Table 1) for site names and localities.

Phylum/Class/Order	Taxa	Site														
		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
Arachnida	Acari	2	2	2	1	2					2		2	2	4	32
Annelida	<i>Eiseniella</i> sp.	2		1	1				1				1	2	1	
Trichoptera	<i>Hydropsyche</i> spp.	12	2			8	1	2	25	114	305	2	103	5		
Megaloptera	<i>Archichauliodes diversus</i>			3		1										
Crustaceae	<i>Austriodotea annectens</i>		14						35			4				
Mollusca	<i>Austropeplea</i> sp.							8								
Diptera	<i>Austrosimulium</i> spp.	3	2	35	4	3	7	8	1	6	1	5		3	14	3
Coleoptera	<i>Berosus</i> sp. (adult)															
Crustaceae	Bosminidae		6		4	2	3		1	3	15	6	2			
Diptera	<i>Brachydeutera</i> sp.					2		2								
Diptera	Ceratopogonidae		2	2		4	10	5			2	2			4	
Diptera	Chironominae A				1								1			
Diptera	<i>Chironomus</i>								3							2
Crustaceae	Chydoridae	5	18	3	108	10	7	105	46		110	2	2	4	3	17
Hexapoda	Collembola		8	2	3	3	3	2		1	7	4	8	4	5	3
Ephemeroptera	<i>Coloburiscus humeralis</i>									7			1			
Diptera	<i>Corynoneura</i> spp.		2	1	2	4		4	1	1	2	4	5	17	93	10
Crustaceae	Cyclopoida	3	3	2	33	5	3	3	2	2	8	5	1	3	8	64
Crustaceae	<i>Daphnia</i> sp.															
Ephemeroptera	<i>Deleatidium</i> spp.	42	16	33	2	194		32	1	193	28	6	16	313	12	

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Coleoptera	Elmidae (adult)	9		1						1				1		
Diptera	Empididae							3		1		2				2
Diptera	<i>Eukiefferiella</i> sp.	132	269	107	318	12	3	34	5	38	85	22	9	33		13
Arachnida	Acarina (Gasmidae)			1										8		8
Mollusca	<i>Gyraulus corinna</i>						2	1			4				2	
Crustaceae	Harpacticoida	2	6	2	6	3	30	5	2	3	5	5	1	5	3	19
Diptera	<i>Harrisius</i> sp.															
Trichoptera	<i>Helicopsyche albescens</i>	24		100	2			3		670				4		
Diptera	Hexatomini A						2	1								5
Diptera	Hexatomini B							1				2		2		
Annelida	Hirudinea	4													1	
Trichoptera	<i>Hudsonema alienum</i>									2	7		1			
Trichoptera	<i>Hudsonema amabile</i>	4	5	3	20	8	1	3	3	3	5		2	13	5	8
Arachnida	Hydracarina	1		1		2		4	2	5	1		1			
Trichoptera	<i>Hydrobiosis frater</i>	2											2			
Coleoptera	<i>Hydora</i> sp.	28	2	5				1		2	6			24	66	2
Trichoptera	<i>Hydrobiosis parumbripennis</i>	3	4		2	2		8		2	7		3	1		
Coleoptera	Hydraenidae		2			2	1			1	3		1		1	
Trichoptera	Hydrobiosidae	3	4	6	2			2		1	2		4	2		
Trichoptera	<i>Hydrobiosis</i> spp.	10		4		2	1	6		2	10		2	3		2
Trichoptera	<i>Hydrobiosis umbripennis</i>				2											
Trichoptera	Hydroptilidae	2	5	2	6	17	8	14	7	3	3	4	2	3	8	16
Crustaceae	Ilyocryptidae						66				1	2			2	27
Coleoptera	<i>Lancetes</i> sp. (larvae)							1								
Ephemeroptera	<i>Leptophlebiidae</i>			3									34		1	
Coleoptera	<i>Liodes</i> <i>deflectus</i> (adult)		5								2					2
Coleoptera	<i>Liodes</i> sp. (larvae)								1						5	7
Coleoptera	<i>Liodes</i> <i>plicatus</i> (adult)									1						

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Diptera	<i>Maoridiamesa</i> sp.	2	132	33				7	1	3	39					31
Hemiptera	<i>Microvelia macgregori</i>	3	5	17	4	3		4			7	2	1	2		
Diptera	<i>Mischoderus</i> spp.												1			8
Diptera	Muscidae		2		2											6
Mollusca	<i>Musculium</i> sp.	1	7	1	7	7	16	3	33		3	2			4	70
Nematoda	Nematoda A	4	33	20	14	4	52	8	2	2	11	4	2	2	64	109
Nematoda	Nematoda B	3	13	7	9	2		2	5	1	4	4			1	4
Nematoda	Nematoda C	2	16	38	3	10	115	31	5	5	34	3	2	10	7	39
Nematoda	Nematoda D											12		2		
Ephemeroptera	<i>Neozephlebia scita</i>			3						1			7			
Trichoptera	<i>Neurochorema confusum</i>					2		2		3	8		2			
Trichoptera	<i>Neurochorema forsteri</i>															
Trichoptera	<i>Oecetis unicolor</i>								2		1					4
Trichoptera	<i>Oeconeus similis</i>							1		1			2			
Oligochaetae	Oligochaeta	4	30	20	30	17	32	7	10	6	36	5	4	23	23	36
Trichoptera	<i>Olinga feredayi</i>	4		19		2		1		28			27			
Arachnida	Acarina (Orbatei)	6	2	3	2	5	2	21	2	3	3	3	10	7	6	9
Diptera	Orthocladiinae	41	186	88	271	13	12	785	18	12	120	27	8	13	8	43
Crustaceae	Ostracoda A		23	9	3	4	15	59	98	7	3	6	1	2	9	8
Crustaceae	Ostracoda D	9	50	64	33	20	213	278	318	28	18	582	3	79	110	279
Crustaceae	Ostracoda F	2	13		3	6	26	40	97	6		80		6	2	
Crustaceae	Ostracoda G	3	9	1	5	3	78	31	74	3	29	11		8	15	125
Crustaceae	Ostracoda H															
Crustaceae	Ostracoda X						8				2					
Trichoptera	<i>Oxyethira albiceps</i>	3	10	8	13	14	36	52	3	5	7	3	6	10	7	11
Diptera	<i>Paradixa</i> spp.					2		1			1				2	4
Crustaceae	Paraleptamphopidae									4		4				
Crustaceae	<i>Paracalliope fluviatilis</i>	2	528		54	34	76	105	45	4	9	196		4		11

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[illegible]

TABLE 1. Continued. PART B: Sites 16-30. See Appendix A (Table 1) for site names and localities.

Phylum/Class/Order	Taxa	Site																	
		16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.			
Arachnida	Acari	2	45	2	1	17	4	3	5	4			1			1			
Annelida	<i>Eiseniella</i> sp.	3		2	3				6	3	5		1	3					
Trichoptera	<i>Hydropsyche</i> spp.	485	5	102	82	8	2		173	94	174	2	110	208	1	24			
Megaloptera	<i>Archichauliodes diversus</i>																		
Crustaceae	<i>Austridotea annectens</i>													15					
Mollusca	<i>Austropeplea</i> sp.								1										
Diptera	<i>Austrosimulium</i> spp.		8	5	8	14	20			2	10	3	7	6					
Coleoptera	<i>Berosus</i> sp. (adult)				1											1			
Crustaceae	Bosminidae		38	23		10	2		1			3		5	4	2			
Diptera	<i>Brachydeutera</i> sp.											2							
Diptera	Ceratopogonidae						2	2				3							
Diptera	Chironominae A		2					4											
Diptera	<i>Chironomus</i>	1					3	6							1				
Crustaceae	Chydoridae	319	34	13	6	69	70	71	4		2	11	2	9	6	4			
Hexapoda	Collembola	3	4	3	1	10	2		69	6	5		2			6			
Ephemeroptera	<i>Coloburiscus humeralis</i>			1						3	6			4					
Diptera	<i>Corynoneura</i> spp.	12	5	3	2	9	8	17	1	2		2	3	7	1				
Crustaceae	Cyclopoida	6	4	22	5	17	4	22	3			8	1	16	3	1			
Crustaceae	<i>Daphnia</i> sp.	8				6									2				
Ephemeroptera	<i>Deleatidium</i> spp.	352		10	4	4	3		108	121	340	2	210	201	2	322			
Coleoptera	Elmidae (adult)	1								2									
Diptera	Empididae	1	107		2	16	2		1	8				8	1				

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Diptera	<i>Eukiefferiella</i> sp.	16	3	45	25	143	13		36	2	8		26	134	20	3
Arachnida	Acarina (Gasmidae)		28			96			1	12						
Mollusca	<i>Gyraulus corinna</i>	4						9	23				1			
Crustaceae	Harpacticoida	1	5	7	20	14	9	15	9	2		4	1	23	1	
Diptera	<i>Harrisius</i> sp.								2						1	
Trichoptera	<i>Helicopsyche albescens</i>								1	2	506		1	10		
Diptera	Hexatomini A	1					2						3			
Diptera	Hexatomini B									2			2			
Annelida	Hirudinea			1							6		1			
Trichoptera	<i>Hudsonema alienum</i>	1		2	20					11						
Trichoptera	<i>Hudsonema amabile</i>	7		1	41			4	4	3	10	11	3	43	1	4
Arachnida	Hydracarina	10	1	5	4			3	10		8		7	8		
Trichoptera	<i>Hydrobiosis frater</i>	2											1	4		
Coleoptera	<i>Hydora</i> sp.	7		2	58				30	18	37	4	9	101		1
Trichoptera	<i>Hydrobiosis parumbripennis</i>	5		5	1	3	1		4	3	3		5	2	2	
Coleoptera	Hydraenidae				1	2			2				1			
Trichoptera	Hydrobiosidae	5		5	8	4	4		5	13	4		2	4	1	
Trichoptera	<i>Hydrobiosis</i> spp.	15		3	5	4			11	6	12		2	12	4	2
Trichoptera	<i>Hydrobiosis umbripennis</i>						1									
Trichoptera	Hydroptilidae	12	10	3	4	6	30	80	9	2			1	8	6	1
Crustaceae	Ilyocryptidae	1		2	2	4		8	1			2				
Coleoptera	<i>Lancetes</i> sp. (larvae)				2											
Ephemeroptera	<i>Leptophlebiidae</i>	22							17	13	21		5	71		5
Coleoptera	<i>Liodessus deflectus</i> (adult)	1											1			
Coleoptera	<i>Liodessus</i> sp. (larvae)															
Coleoptera	<i>Liodessus plicatus</i> (adult)												1	1		
Diptera	<i>Maoridiamesa</i> sp.	6		4		6				2			2			
Hemiptera	<i>Microvelia macgregori</i>	1	4		1	10	5	4	4	2	5	2	1			1

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Diptera	<i>Mischoderus</i> spp.	1		1			2			4						
Diptera	Muscidae						2				1	2				
Mollusca	<i>Musculium</i> sp.				9		40	2	3	4	5		7	1		
Nematoda	Nematoda A	3	3		23	21	16	90	3	2	6	258	4	7	4	
Nematoda	Nematoda B			1	12	24	2	4	2	1			5		2	
Nematoda	Nematoda C	4	2		5	9	9	5	9			123	4	38	2	
Nematoda	Nematoda D					4		21		2						
Ephemeroptera	<i>Neozephlebia scita</i>								2	11				23		
Trichoptera	<i>Neurochorema confusum</i>	14		2	4	3			3	2	1		2	4	3	
Trichoptera	<i>Neurochorema forsteri</i>	2									1					
Trichoptera	<i>Oecetis unicolor</i>			1												
Trichoptera	<i>Oeconeus similis</i>			1	1					2				3		
Oligochaetae	Oligochaeta	5	48	13	18	187	21	40	24	8	7	25	4	24	7	2
Trichoptera	<i>Olinga feredayi</i>	4			12				28	6	8		109	84		33
Arachnida	Acarina (Orbatei)	12	115	5	1	110	8	4	6	7	4	4	1	24	17	1
Diptera	Orthocladiinae	29	334	9	27	378	577	65	7	41	13	12	2	220	12	1
Crustaceae	Ostracoda A	1		1	25		17		6	3	10	134	2	17	13	
Crustaceae	Ostracoda D	25	14	3	9	44	42	172	59	6	4	558		142	9	1
Crustaceae	Ostracoda F	5		3	7	4	2	17	4	2			3	9	1	
Crustaceae	Ostracoda G	26	7	4	21	6	161	282	4	1	2	388	1	31	2	1
Crustaceae	Ostracoda H						6	5						4		
Crustaceae	Ostracoda X	12		59				7	1				1			
Trichoptera	<i>Oxyethira albiceps</i>	26	13	3	3	25	10	140	7	2	3	12	2	6	16	3
Diptera	<i>Paradixa</i> spp.		4	4	2		5	4						2		
Crustaceae	Paraleptamphopidae									1						4
Crustaceae	<i>Paracalliope fluviatilis</i>		17	17	4	294	29	47	2	44			3	206	97	4
Diptera	<i>Paradixa fuscinervis</i>						4			2						
Trichoptera	<i>Paroxyethira</i> spp.	4						10								

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Diptera	<i>Paradixa tonnoiri</i>												1	3		
Diptera	<i>Polypedilum</i>					1		8			4			3		
Crustaceae	<i>Phreatogammarus</i>					1				2			3	8		2
Mollusca	<i>Physa</i> sp.	9		3	3	1		66	11		1	24	1	8	3	
Trichoptera	<i>Polyplectropus puerilis</i>	2		1			2									2
Mollusca	<i>Potamopyrgus antipodarum</i>	7	6	86	1173	131	10	70	79	247	250	392	33	155	172	20
Trichoptera	<i>Psilochorema bidens</i>	12	16	1	10	3	3		3	7	8		5	36	4	3
Trichoptera	<i>Psilochorema nemarole</i>				1								1			
Diptera	Psychodidae		5		4				2					8		
Trichoptera	<i>Pycnocentroides</i> sp. A					120	2						164			157
Trichoptera	<i>Pycnocentroides</i> spp.	284	2	222	490	115	4	2	25	147	319		175	576	15	131
Trichoptera	<i>Pycnocentria</i> spp.	30	1	78	46	264	6		188	256	39		145	660	10	159
Platyhelminthes	Rhabdocoela				2			21							7	
Hemiptera	<i>Saldula</i> sp.					4							1			
Diptera	<i>Scatella</i> sp.	1				4	3								1	
Coleoptera	Scirtidae												1			
Hemiptera	<i>Sigara arguta</i>	2				2		5	2			3	1			1
Crustaceae	<i>Simocephalus</i> sp.	8				34		10					1		2	
Coleoptera	Staphylinidae			1												
Diptera	<i>Stictocladius</i> sp.	4					2									
Diptera	Tanypodinae	2		2	20	5	10	6	3		2	2	1	7		1
Diptera	<i>Tanytarsini</i> spp.	4	2	6	2	36	23	8	2						8	
Trichoptera	<i>Triplectides</i> sp.	1		1	2	4	2			6		5			3	
Platyhelminthes	Turbellaria				1			1		5					1	
Odonata	<i>Xanthocnemis zealandica</i>		4				4								1	1
Plecoptera	<i>Zelandobius confusum</i>		2								3					

TABLE E2. Results from partial redundancy analysis (*p*RDA) of invertebrate community abundance constrained by sediment after removing the covarying effects of nitrate and spatial location (conditioning variables). Taxa scores (*p*RDA Axes 1 and 2) are scaled proportional to eigenvalues. SIS, suspendable inorganic sediment.

Phylum/Class/Order	Taxa	<i>p</i> RDA Axis 1	<i>p</i> RDA Axis 2
Ephemeroptera	<i>Deleatidium</i> spp.	-0.3045	0.0873
Trichoptera	<i>Pycnocentrodes</i> spp.	-0.2782	-0.0587
Trichoptera	<i>Pycnocentria</i> spp.	-0.2541	-0.1043
Trichoptera	<i>Hydropsyche</i> spp.	-0.1778	0.0204
Trichoptera	<i>Helicopsyche albescens</i>	-0.1641	0.1735
Trichoptera	<i>Olinga feredayi</i>	-0.1323	-0.0020
Trichoptera	<i>Pycnocentrodes</i> sp. A	-0.1255	-0.0089
Diptera	<i>Eukiefferiella</i> spp.	-0.1107	0.0841
Ephemeroptera	Leptophlebiidae	-0.0661	-0.0482
Trichoptera	<i>Hydrobiosis parumbripennis</i>	-0.0336	0.0073
Hexapoda	Collembola	-0.0331	-0.0169
Coleoptera	<i>Hydora</i> sp.	-0.0331	0.0022
Trichoptera	Hydrobiosidae	-0.0305	-0.0158
Trichoptera	<i>Hydrobiosis</i> spp.	-0.0271	0.0203
Trichoptera	<i>Psilochorema bidens</i>	-0.0258	-0.0132
Arachnida	Hydracarina	-0.0253	0.0075
Trichoptera	<i>Neurochorema confusum</i>	-0.0221	-0.0038
Ephemeroptera	<i>Coloburiscus humeralis</i>	-0.0204	-0.0052
Trichoptera	<i>Hudsonema amabile</i>	-0.0196	-0.0083
Crustacea	<i>Phreatogammarus</i> sp.	-0.0186	-0.0087
Annelida	<i>Eisenella</i> sp.	-0.0175	0.0020
Hemiptera	<i>Microvelia macgregori</i>	-0.0173	-0.0035
Ephemeroptera	<i>Neozephlebia scita</i>	-0.0154	-0.0292
Diptera	Paraleptamphopidae	-0.0142	0.0124
Annelida	Hirudinea	-0.0123	0.0178
Trichoptera	<i>Hydrobiosis frater</i>	-0.0123	0.0028
Coleoptera	<i>Liodessus plicatus</i> (adult)	-0.0083	0.0027
Coleoptera	Hydraenidae	-0.0083	-0.0005
Diptera	<i>Polypedilum</i> sp.	-0.0074	-0.0279
Nematoda	Nematoda B	-0.0069	0.0129
Coleoptera	Elmidae (adult)	-0.0067	0.0314
Diptera	<i>Paradixa tonnoiri</i>	-0.0063	-0.0115
Diptera	<i>Paradixa fuscinervis</i>	-0.0062	-0.0020
Plecoptera	<i>Zelandobius confusus</i>	-0.0062	-0.0064
Coleoptera	Scirtidae	-0.0061	0.0108
Coleoptera	<i>Berosus</i> sp. (adult)	-0.0051	-0.0020

Diptera	Psychodidae	-0.0048	-0.0228
Diptera	<i>Harrisius</i> sp.	-0.0045	0.0013
Trichoptera	<i>Hydrobiosis umbripennis</i>	-0.0045	0.0013
Trichoptera	<i>Psilochorema nemorale</i>	-0.0044	-0.0020
Trichoptera	<i>Neurochorema forsteri</i>	-0.0041	0.0022
Crustacea	<i>Daphnia</i> sp.	-0.0039	-0.0007
Trichoptera	<i>Oeconesus similis</i>	-0.0039	-0.0151
Diptera	<i>Stictocladius</i> sp.	-0.0028	0.0036
Trichoptera	<i>Hudsonema alienum</i>	-0.0027	-0.0177
Coleoptera	<i>Liodessus deflectus</i> (adult)	-0.0024	0.0014
Hemiptera	<i>Saldula</i> sp.	-0.0015	-0.0036
Diptera	Muscidae	-0.0015	-0.0004
Crustacea	Ostracoda H	-0.0013	-0.0140
Coleoptera	Staphylinidae	0.0006	-0.0098
Megaloptera	<i>Archichauliodes diversus</i>	0.0009	0.0007
Diptera	<i>Scatella</i> sp.	0.0011	0.0008
Diptera	Tanypodinae	0.0012	-0.0048
Diptera	Chironominae A	0.0020	-0.0181
Trichoptera	<i>Polyplectropus puerilis</i>	0.0021	0.0096
Platyhelminthes	Turbellaria	0.0025	0.0099
Coleoptera	<i>Lancetes</i> sp. (larvae)	0.0028	-0.0021
Diptera	<i>Brachydeutera</i> sp.	0.0033	0.0031
Diptera	<i>Mischoderus</i> spp.	0.0053	-0.0124
Mollusca	<i>Austropeplea</i> sp.	0.0056	0.0047
Trichoptera	<i>Paroxyethira</i> spp.	0.0065	-0.0058
Odonata	<i>Xanthocnemis zealandica</i>	0.0065	-0.0021
Crustacea	<i>Simocephalus</i> sp.	0.0066	-0.0119
Diptera	Hexatomini B	0.0079	-0.0016
Mollusca	<i>Gyraulus corinna</i>	0.0079	-0.0001
Crustacea	Bosminidae	0.0082	-0.0266
Nematoda	Nematoda D	0.0112	-0.0231
Diptera	<i>Maoridiamesa</i> spp.	0.0115	0.0145
Diptera	<i>Chironomus</i> spp.	0.0119	0.0017
Arachnida	Acari	0.0121	-0.0399
Arachnida	Acari (Gasmidae)	0.0125	-0.0517
Crustacea	<i>Austridotea annectens</i>	0.0148	0.0269
Trichoptera	<i>Oecetis unicolor</i>	0.0149	0.0072
Trichoptera	<i>Triplectides</i> sp.	0.0151	-0.0012
Arachnida	Acari (Orbatei)	0.0172	-0.0484
Diptera	Empididae	0.0173	-0.0489
Diptera	<i>Paradixa</i> spp.	0.0184	-0.0251
Diptera	Hexatomini A	0.0194	0.0049
Coleoptera	<i>Liodessus</i> spp. (larvae)	0.0196	0.0056

Diptera	<i>Austrosimulium</i> spp.	0.0199	0.0080
Diptera	<i>Tanytarsini</i> spp.	0.0231	0.0411
Hemiptera	<i>Sigara arguta</i>	0.0248	0.0007
Crustacea	Ostracoda X	0.0294	-0.0284
Crustacea	<i>Paracalliope fluviatilis</i>	0.0351	-0.0454
Trichoptera	Hydroptilidae	0.0355	-0.0206
Crustacea	Cyclopoida	0.0364	-0.0192
Platyhelminthes	Rhabdocoela	0.0375	-0.0098
Diptera	<i>Corynoneura</i> spp.	0.0381	-0.0424
Diptera	Ceratopogonidae	0.0391	0.0063
Annelida	Oligochaeta	0.0462	-0.0521
Crustacea	Harpacticoida	0.0489	-0.0223
Mollusca	<i>Physa acuta</i>	0.0503	-0.0335
Crustacea	Chydoridae	0.0547	0.0295
Diptera	Orthoclaadiinae	0.0598	-0.0332
Trichoptera	<i>Oxyethira albiceps</i>	0.0624	-0.0339
Crustacea	Ostracoda F	0.0750	0.0790
Crustacea	Ostracoda A	0.0752	0.0645
Mollusca	<i>Musculium</i> sp.	0.0789	0.0131
Crustacea	Ilyocryptidae	0.0889	-0.0090
Nematoda	Nematoda A	0.1149	-0.0321
Nematoda	Nematoda C	0.1205	0.0238
Mollusca	<i>Potamopyrgus antipodarum</i>	0.1650	-0.0979
Crustacea	Ostracoda G	0.1776	-0.0003
Crustacea	Ostracoda D	0.3167	0.1285
Contribution of eigen-values to the variance after removing the contribution of conditioning variables		% Variation	
		23.5	5.3
Contribution of accumulated constrained eigen-values to the variance		% Variation	
		66.4	14.9
<i>Bi-plot scores for constraining variables</i>			
% Sediment cover (reach)		0.64	0.08
% Sediment cover (patch)		0.62	0.13
log SIS (g/m ²)		0.42	-0.44
log Sediment depth (mm)		0.57	-0.07

APPENDIX F. Relationships of measured variables used for deposited sediment index.

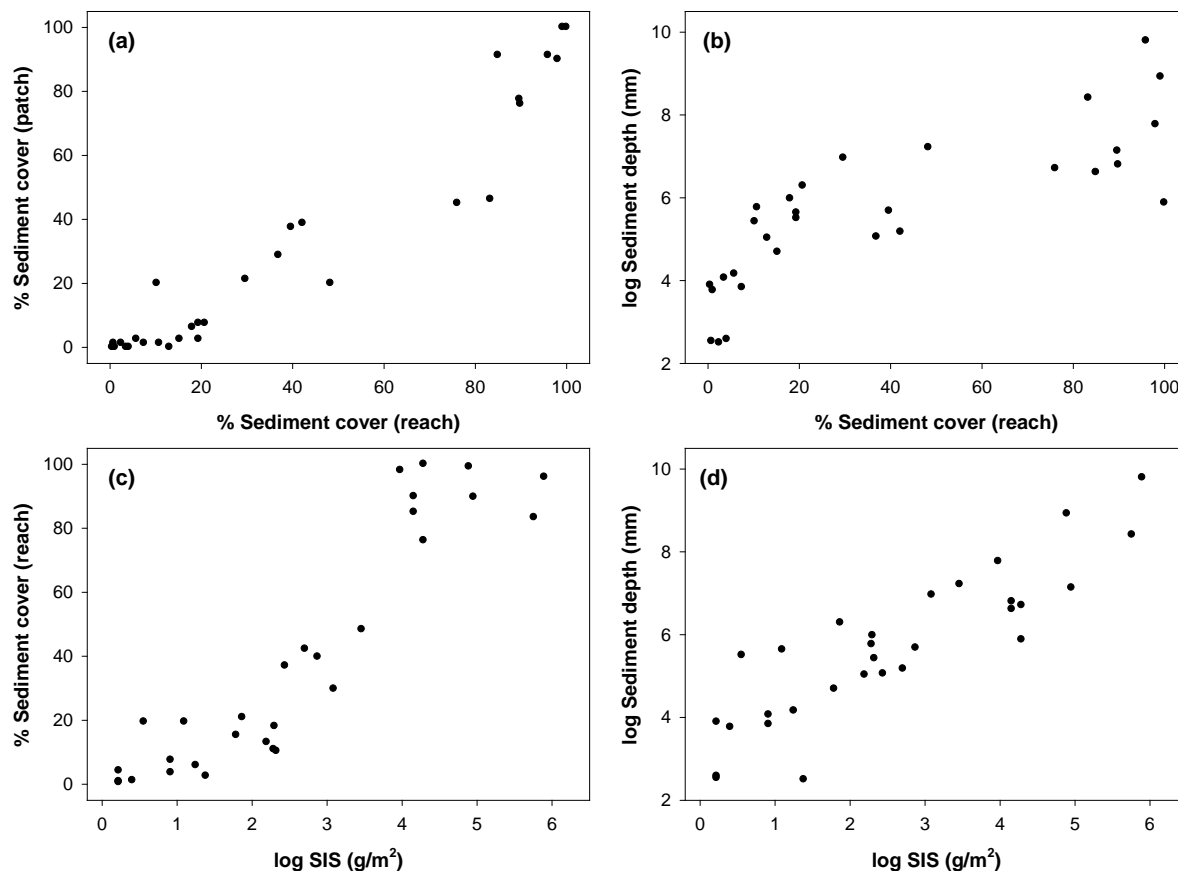


FIG. 1. Relationships of selected sediment parameters recorded from 30 streams sampled streams surveyed across the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. (a) Patch and reach % sediment cover were strongly correlated (Spearman's Rank correlation, $\rho = 0.94$, $P < 0.001$), as was (b) sediment depth and reach sediment cover ($\rho = 0.90$, $P < 0.001$). Likewise, SIS (g/m^2) was strongly correlated (c, d) with these two measures respectively ($\rho = 0.87$, $P < 0.001$; $\rho = 0.87$, $P < 0.001$). SIS, suspendable inorganic sediment.

APPENDIX G. AIC_c values used to select univariate regression models.TABLE 1. AIC_c values of models used to investigate the relationship of selected sediment predictor variables to the relative abundance of sediment-sensitive taxa (% EPT). SIS: suspendable inorganic sediment.

Response	Variable	Model			
	Predictor	Linear	Exponential	Asymptotic exponential	4-parameter sigmoidal
% EPT	Sediment (PC1)	244.0	234.7	236.4	227.8
	log SIS (g/m ²)	259.6	261.6	263.3	257.7
	% Sediment cover (reach)	244.9	230.5	233.0	228.9
	% Sediment cover (patch)	254.9	228.8	228.0	230.6

Akaike Information Criterion (AIC) is a measure of the relative goodness of fit for a statistical model. Given a set of candidate models for the data, the preferred model is the one with the minimum AIC value. AIC_c is AIC with a correction for finite sample sizes and the number of parameters used (Burnham & Anderson, 2002).

LITERATURE CITED

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

APPENDIX H. Results of change-point analyzes identifying sediment thresholds.

TABLE 1. Change-point analyzes (CPA) for the relative abundance of sediment-sensitive taxa (% EPT) in response to measured aspects of deposited fine inorganic sediment. SIS: suspendable inorganic sediment.

Response	Predictor	Change-point	95% confidence interval	Probability of change	Level	Group means
% EPT	Sediment (PC1)	-0.31	-0.31, -0.33	100%	1	65, 10
	log SIS (g/m ²)	155	63, 244	99%	1	67, 32
	% Sediment cover (reach)	21	18, 21	100%	2	63, 9
	% Sediment cover (patch)	13	4, 13	100%	1	61, 11

APPENDICES

CHAPTER 3

APPENDIX A. Detailed descriptions of data collection methods.

A.1 Riparian vegetation

The dominant vegetation types on the Canterbury Plains are pasture (introduced grasses and *Trifolium* spp.) and monocultures of crops, interspersed with windbreaks and hedgerows of introduced conifers (*Cupressus* and *Pinus* spp.), and members of the Salicaceae including poplars (*Populus* spp.) and willows (*Salix* spp.). These vegetation types also form the principal forms of riparian plantings.

A.2 Study site selection

Twelve first to third order perennial streams were selected into six categories of dissolved nutrients and deposited sediment (i.e., a two by three factorial design incorporating differing levels of nutrients and sediment). Differing levels of nutrients were used to help avoid confounding sediment effects with that of enrichment, and to realistically reflect the environmental conditions present in our study region. Nutrient status in streams was determined from spot measures of specific conductivity (YSI 63, YSI Incorporated, Yellow Springs, OH, USA); conductivity is strongly correlated with total nitrate concentrations in our study region (Greenwood et al. 2012). Nutrient status was categorized as ‘low’ ($<110 \mu\text{S}_{25^\circ}\text{C/cm}$) and ‘medium-high’ ($\geq 110 \mu\text{S}_{25^\circ}\text{C/cm}$). Fine inorganic sediment ($<2 \text{ mm}$ in diameter) deposited on the streambed was categorized as ‘low’ ($<15\%$), ‘medium’ ($15\text{-}50\%$), and ‘high’ ($> 50\%$) cover. Visual estimates of cover made from the banks are strongly correlated with physical measures of deposited fine inorganic sediment (Clapcott et al. 2011).

A.3 Physicochemical data collection

The collection of physicochemical data, including measurements of deposited fine sediment, followed the same protocols outlined in Burdon et al. (in press); however, these are

reported below for the reader's convenience. In each reach, mean depth and flow velocity (Marsh-McBirney Flo-Mate Model 2000, Hach, Loveland, CO, USA) were calculated from measurements at ten equidistant points across three transects; stream widths were also recorded at these locations. Spot measurements were made of pH/specific conductivity (YSI 63), dissolved oxygen (% saturation), and temperature (YSI 550A). Water samples were collected on both sampling dates for chemical analysis, and consisted of filtered (LabServ® GF/F, 25 mm Ø; Thermo Fisher Scientific New Zealand Ltd, North Shore City, NZ) stream water (100 ml) collected in opaque acid-washed bottles, which were placed on ice, and then later frozen prior to analysis. Samples were analyzed for nitrate (nitrate and nitrite nitrogen; mg/L) and DRP (dissolved reactive phosphorus; µg/L) using a SYSTEAs Easychem discrete colorimetric auto-analyzer (SYSTEAs S.p.A., Anagni, Italy). Ammonia concentrations were not analyzed as previous research in these streams has shown ammonia levels to be very low (Greenwood et al. 2012). Nitrate was analyzed using the cadmium reduction method and DRP using the molybdate reduction method (APHA 1995). A further 1 L water sample was collected from each site for estimation of total suspended solids (g/L), refrigerated upon return to the laboratory, and processed within 48 hours of collection by filtering through a pre-ashed, pre-weighed glass fibre filter (LabServ® GF/F, 47 mm Ø) prior to drying (50° C, 24 hours), weighing, ashing (550° C, 6 hours), and re-weighing.

To quantify sediment cover (and substrate composition) within each 'reach', ten 0.09 m² quadrats were selected within the stream reach in a stratified-random manner (Niyogi et al. 2007); substrate composition was assessed visually. Two methods were used to assess substrate composition within a gridded quadrat placed on the streambed. Using a glass viewing-window, the dominant substrate at 25 points using the grid intersections was recorded, whereas the second method characterized the dominant substrate within each of 16

grids. Substrate class assessment was based on the Wentworth scale (Wentworth 1922).

These methods were repeated at each 'patch' where Surber samples were collected.

Sediment depth was recorded at ten points in each reach using a stratified random selection process (Niyogi et al., 2007). A ruler was inserted into soft sediment until underlying, coarser substratum was reached. Suspendable inorganic sediment (SIS; g/m²) was estimated using the Quorer method (Quinn and Cooper 1997). The benthic substrate in an open drum (30 cm Ø, 0.07 m²) at 15 random locations within the 30 m reach was vigorously disturbed using a steel rod (duration of 30 seconds) to collect 15 replicate samples of suspendable sediment (i.e., a 250 ml water sample taken from the water column inside the open drum). They were processed within 48 hours of collection. To collect the coarsest suspendable sediment, water samples were first filtered through a 125-µm Endecott sieve (Endecotts Limited, London, UK). The material collected in the sieve was then washed into a pre-weighed aluminum dish and dried, weighed, ashed, and re-weighed. To collect the finer suspendable sediment grains, a sub-sample (50 ml) of the sieved water sample was then filtered through a pre-ashed, pre-weighed filter (LabServ[®] GF/F, 47 mm Ø), before undergoing the same process. These two estimates of fine inorganic sediment (≥ 125 µm and < 125 µm) were combined (minus the background concentrations of suspended sediment estimated from a 1 L sample of stream water) to give an estimate of total SIS (g/m²).

A.4 Basal resources

Basal resources were collected from stream reaches for stable isotope analyses and estimation of resource quality and availability. Suspended fine particulate matter (SFPM) was collected using a plankton net (45 µm mesh) suspended in the water column for ten minutes and stored on ice until being frozen in the laboratory. Thawed sub-samples (50 ml) were filtered through a pre-ashed, pre-weighed filter (LabServ[®] GF/F, 47 mm Ø), dried (48 hours,

50° C), weighed, ashed (6 hours, 550° C), and re-weighed to estimate organic content (resource availability). Fine and coarse benthic organic matter (g/m^2 FBOM and CBOM respectively) was estimated from material collected in Surber samples. Material was elutriated, separated using a 2 mm Endecott sieve, dried (48 hours, 50° C), weighed, ashed (4 hours, 550° C), and re-weighed. Dried samples of SFPM, FBOM, and CPOM were retained for stable isotopes analysis (SIA).

To estimate periphyton/biofilm availability (% organic matter and chlorophyll-*a*), five cobbles or sediment samples were collected from random locations. Where fine sediment occurred in large deposits, a glass petri dish (45 mm Ø) was used to remove a circular section of sediment from the stream bed to 7.5 mm deep (Biggs and Kilroy 2000). Individual samples were wrapped in foil, and stored on ice before being frozen. Cobbles or sediment samples were immersed in 100% ethanol for 24 hours (in the dark) at 10° C for pigment extraction. Chlorophyll-*a* was analyzed using the methods for spectrophotometry outlined in Biggs and Kilroy (2000). Filtered sub-samples (LabServ[®] GF/C, 47 mm Ø) of periphyton (brushed from stones in ethanol) and sediment samples (45 µm Endecott sieve) were dried, weighed, ashed, and re-weighed to estimate % organics. The stones surface area was calculated using the equation of Biggs and Kilroy (2000). Additional cobbles ($n = 10$) were collected for SIA of periphyton/biofilms; stone surfaces were scraped using a scalpel before drying.

Other potential carbon sources collected for SIA, including filamentous algae were collected by hand, placed on ice and frozen. Basal resource quality was estimated by calculating the ratio of molar carbon to nitrogen; bulk values of C and N were obtained from samples analyzed on a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility (University of California, Davis, CA, USA).

A.5 Invertebrate indices and traits

Additional structural indices used included the relative abundance and richness of EPT taxa from the insect families Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies); these are commonly used indices of stream health (Boothroyd and Stark 2000). We used functional-feeding groups (FFGs) to help describe changes to invertebrate communities and food webs along the sediment gradient. FFGs are well-established as a means to describe the functional roles of stream invertebrates; which can often display a high degree of polyphagy (Cummins 1973). Based on invertebrate trait data from the New Zealand Freshwater Biodata Information System (FBIS), we assigned invertebrate trait affinity scores using ‘fuzzy-coding’ (Chevenet et al. 1994) to four FFGs; ‘predators’, ‘shredders’ (including ‘gougers’; detritivores that consume coarse organic matter), ‘grazers’ (including ‘scrapers’), and ‘collectors’ (including ‘gatherers’ and ‘filter-feeders’). Filter-feeders were analyzed separately, but these results are not presented because they were strongly influenced by one sediment-sensitive taxon, the net-building caddisfly *Hydropsyche colonica* (Hydropsychidae). Invertebrate taxa were assigned trait affinity scores from 0 (absent) to 3 (strong affinity) using the ‘fuzzy-coding’ approach.

These scores were used with invertebrate community data to calculate trait frequencies (i.e., trait abundances) and mean affinities (relative trait frequencies; i.e., trait frequency per individual or taxon). To distinguish more specialized taxa from generalist fauna, we only included invertebrates with strong trait affinities (i.e., ≥ 2) for regression analyses of the four FFGs. Additional feeding trait information generated from these data included taxa that engaged in omnivory (taxa that scored in predatory and primary consumer FFGs) and polyphagy (taxa that scored in more than one primary consumer FFG); traits scored presence (1) or absence (0). Additional feeding traits based on habitat associations were included using ‘fuzzy-coding’ trait affinity scores from 0 (absent) to 3 (strong affinity);

these described taxa strongly associated with rheophilic (i.e., hard-bottomed riffle habitat) or depositional/fine substrate habitats, including predators (e.g., Diptera: Ceratopogonidae: Ceratopogoninae as a deposit-feeding predator; Benke et al. 1984).

LITERATURE CITED

- American Public Health Association (APHA). 1995. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC, USA.
- Benke, A. C., T. C. J. Arsdall, D. M. Gillespie, and F. K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25-63.
- Biggs, B. J. F., and C. Kilroy. 2000. Stream periphyton monitoring manual. Ministry for the Environment, Wellington, NZ.
- Boothroyd, I., and J. D. Stark 2000. Use of invertebrates in monitoring. Pgs 344-373 in *New Zealand stream invertebrates: ecology and implications for management*. M. J. Winterbourn and K. J. Collier (eds.). New Zealand Limnological Society, Christchurch, NZ.
- Chevenet, F., S. Dolédec, and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31:295-309.
- Clapcott, J. E., R. G. Young, J. S. Harding, C. D. Matthaei, J. M. Quinn, and R. G. Death. 2011. Sediment assessment methods: protocols and guidelines for assessing the effects of deposited fine sediment on in-stream values. Cawthron Institute, Nelson, NZ.
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* 18:183–206.

- Greenwood, M. J., J. S. Harding, D. K. Niyogi, and A. R. McIntosh. 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology* 49:213-222.
- Quinn, J. M., and A. B. Cooper. 1997. Land–water interactions at Whatawhata, New Zealand: introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research* 31:569–577.
- Niyogi, D., M. Koren, C. Arbuckle, and C. Townsend. 2007. Stream communities along a catchment land-use gradient: subsidy-stress responses to pastoral development. *Environmental Management* 39:213-225.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* 30:377-392.

TABLE A2. ‘Fuzzy-coded’ trait affinity scores for stream invertebrates collected from 12 streams surveyed on the Canterbury Plains, South Island, New Zealand during the austral summer of 2009-2010. SHD, ‘Shredders’; GRZ, ‘Grazers’; COL, ‘Collectors’; PRD, ‘Predators’; OMN, ‘Omnivores’; PLY, ‘Polyphages’; DFD, ‘Deposit-feeder’; RHP, ‘Rheophiles’.

Invertebrates		Functional-feeding group				Feeding generalists		Habitat	
Phylum/Class/Order	Taxa	SHD	GRZ	COL	PRD	OMN	PLY	DFD	RHP
Arachnida	Acari			1	2	1		3	
Annelida	<i>Eisenella</i> sp.			3				3	
Trichoptera	<i>Hydropsyche</i> spp.			2	1	1			1
Megaloptera	<i>Archichauliodes diversus</i>				3				3
Crustacea	<i>Austridotea annectens</i>	1		1	1	1	1	1	
Mollusca	<i>Austropeplea</i> sp.		1	2			1		
Diptera	<i>Austrosimulium</i> spp.			3					
Coleoptera	<i>Berosus</i> sp. (adult)			1	2	1			
Crustacea	Bosminidae			3				3	
Diptera	<i>Brachydeutera</i> sp.		1	2			1		
Diptera	Ceratopogonidae				3			3	
Diptera	Chironominae A			3				3	
Diptera	<i>Chironomus</i> spp.			3				3	
Crustacea	Chydoridae			3				3	
Coleoptera	Coleoptera			3				1	
Hexapoda	Collembola			3					
Ephemeroptera	<i>Coloburiscus humeralis</i>			3					2
Diptera	<i>Corynoneura</i> spp.			3				1	
Crustacea	Cyclopoida			3				1	
Crustacea	<i>Daphnia</i> sp.			3					
Ephemeroptera	<i>Deleatidium</i> spp.		2	1			1		3
Coleoptera	Elmidae (adult)		2	1			1		3
Diptera	Empididae		1	2			1		
Diptera	<i>Ephydrella</i> sp.		1	2			1		
Diptera	<i>Eukiefferiella</i> spp.		2	1			1		2
Arachnida	Acari (Gasmidae)			3					
Mollusca	<i>Glyptophysa</i> sp.		1	2			1		
Mollusca	<i>Gyraulus corinna</i>		1	2			1		
Crustacea	Harpacticoida			3				3	
Diptera	<i>Harrisius</i> sp.	3							
Trichoptera	<i>Helicopsyche albescens</i>		3						3
Diptera	Hexatomini A				3			2	
Diptera	Hexatomini B				3			2	
Annelida	Hirudinea				3			1	
Trichoptera	<i>Hudsonema alienum</i>	1		1	1	1	1		1

Trichoptera	<i>Hudsonema amabile</i>	1	1	1	1	1	1
Arachnida	Hydracarina			3			2
Trichoptera	<i>Hydrobiosis frater</i>			3			3
Coleoptera	<i>Hydora</i> sp.	2	1			1	3
Trichoptera	<i>Hydrobiosis parumbripennis</i>			3			2
Coleoptera	Hydraenidae	2	1			1	2
Trichoptera	Hydrobiosidae		1	2		1	2
Trichoptera	<i>Hydrobiosis</i> spp.		1	2		1	2
Trichoptera	<i>Hydrobiosis styx</i>			3			2
Trichoptera	Hydroptilidae	1	2			1	
Crustacea	Ilyocryptidae		3				3
Coleoptera	<i>Lancetes</i> sp. (larvae)			3			
Ephemeroptera	Leptophlebiidae	2	1			1	2
Coleoptera	<i>Liodessus deflectus</i> (adult)			3			
Coleoptera	<i>Liodessus</i> spp. (larvae)			3			
Coleoptera	<i>Liodessus plicatus</i> (adult)			3			
Diptera	<i>Maoridiamesa</i> spp.	2	1			1	3
Hemiptera	<i>Microvelia macgregori</i>			3			
Diptera	<i>Mischoderus</i> spp.	2		1	1		2
Diptera	Muscidae		3				2
Mollusca	<i>Musculium</i> sp.		3				2
Nematoda	Nematoda A		3				3
Nematoda	Nematoda B		3				3
Nematoda	Nematoda C		3				3
Ephemeroptera	<i>Neozephlebia scita</i>		3				1
Trichoptera	<i>Neurochorema confusum</i>			3			3
Trichoptera	<i>Neurochorema forsteri</i>			3			3
Trichoptera	<i>Oecetis unicolor</i>		1	2	1		1
Trichoptera	<i>Oeconesus similis</i>	3					1
Annelida	Oligochaeta		3				3
Trichoptera	<i>Olinga feredayi</i>	2	1			1	2
Arachnida	Acari (Orbatei)		3				2
Diptera	Orthocladiinae		3				1
Crustacea	Ostracoda H		3				2
Crustacea	Ostracoda A		3				2
Crustacea	Ostracoda D		3				3
Crustacea	Ostracoda F		3				2
Crustacea	<i>Herpetocypris pascheri</i>		3				2
Crustacea	Ostracoda X		3				2
Crustacea	Ostracoda Y		3				2
Trichoptera	<i>Oxyethira albiceps</i>	2	1			1	1
Trichoptera	<i>Paroxyethira</i> spp.	2	1			1	1
Diptera	<i>Paradixa</i> spp.		3				
Crustacea	<i>Paracrangonyx</i> sp.	1	2			1	3
Diptera	Paraleptamphopidae		3				3
Crustacea	<i>Paranephrops zealandicus</i>		3				

Crustacea	<i>Paratya curvirostris</i>			2	1	1			
Crustacea	<i>Paracalliope fluviatilis</i>	1		2			1	1	
Diptera	<i>Paradixa tonnoiri</i>			3					
Diptera	<i>Polypedilum</i> sp.			3					
Crustacea	<i>Phreatogammarus</i> sp.			2	1		1	1	3
Mollusca	<i>Physa acuta</i>	1	1	1			1		
Platyhelminthes	Turbellaria				3				3
Trichoptera	<i>Polyplectropus puerilis</i>			1	2	1		1	
Mollusca	<i>Potamopyrgus antipodarum</i>		1	2			1		
Trichoptera	<i>Psilochorema bidens</i>				3				2
Trichoptera	<i>Psilochorema nemorale</i>				3				2
Trichoptera	<i>Psilochorema tautoru</i>				3				2
Diptera	Psychodidae			3					
Trichoptera	<i>Pycnocentrodes</i> sp. A		3						3
Trichoptera	<i>Pycnocentrodes</i> spp.		3						3
Trichoptera	<i>Pycnocentria</i> spp.	2		1			1		2
Platyhelminthes	Rhabdocoela			3				3	
Hemiptera	<i>Saldula</i> sp.				3				
Diptera	<i>Scatella</i> sp.		1	2			1		
Hemiptera	<i>Sigara arguta</i>		1	2			1		
Crustacea	<i>Simocephalus</i> sp.			3					
Coleoptera	Staphylinidae			2	1	1			
Diptera	<i>Stictocladius</i> sp.			3					
Plecoptera	<i>Stenoperla prasina</i>				3				3
Diptera	Tanypodinae			1	2	1			
Diptera	<i>Tanytarsini</i> spp.			3					1
Trichoptera	<i>Triplectides</i> sp.	3							
Odonata	<i>Xanthocnemis zealandica</i>				3				3
Diptera	<i>Zelandotipula</i> sp.	1		2			1	2	

APPENDIX B. Primary consumers used to calculate $\delta^{15}\text{N}$ baselines for estimation of MTP.

TABLE 1. Invertebrate prey taxa used to provide a baseline for the calculation of maximum trophic position (MTP). Mean $\delta^{15}\text{N} \pm 1$ standard error. *Deleatidium* sp. and *Neozephlebia scita* (Ephemeroptera: Leptophlebiidae), *Herpetocypris pascheri* (Ostracoda: Cyprididae), *Pycnocentroides* sp. (Trichoptera; Conoesucidae), *Austrosimulium* sp. (Diptera: Simuliidae), Orthocladiinae (Diptera: Chironomidae), *Paracalliope fluviatilis* (Amphipoda: Paracalliopiidae), *Oxyethira albiceps* (Trichoptera: Hydroptilidae). The 3 taxa used from each stream are listed below.

Stream	Primary consumer			Mean $\delta^{15}\text{N}$
Clearwater	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	5.05 ± 1.17
Cridges	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Oxyethira</i>	9.82 ± 0.05
Southbrook	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	7.25 ± 0.08
Cust	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	5.14 ± 0.48
Waihikuawa	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Neozephlebia</i>	4.30 ± 0.15
Northbrook	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	7.85 ± 0.11
Saltwater	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	8.29 ± 0.32
Flaxton	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	6.72 ± 0.76
Shipleys	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	3.70 ± 0.05
Springs	<i>Herpetocypris</i>	<i>Austrosimulium</i>	<i>Paracalliope</i>	4.06 ± 0.23
Easterbrook	<i>Herpetocypris</i>	Orthocladiinae	<i>Paracalliope</i>	6.55 ± 0.52
Courtenay	<i>Deleatidium</i>	<i>Pycnocentroides</i>	<i>Paracalliope</i>	6.92 ± 0.30

APPENDIX C. Detailed descriptions of statistical methods and regression models tested.

C.1 Partial redundancy analysis (*p*RDA)

To test the association of deposited sediment and nutrients with invertebrate and fish community composition, partial redundancy analysis was used (*p*RDA). We used total abundance, total occupancy (presence-absence) and the taxa selected for SIA to create each invertebrate matrix; only occupancy data were used to create the fish matrix. For community analyses, three models were evaluated; sediment (PC1) with nitrate (NO₃-N, mg/l) and phosphorus (dissolve reactive phosphorus, µg/l) separately, and sediment with both nutrients together. An additional model tested the effects of sediment (PC1) and primary community composition (NMDS Axis 1 scores) on the relative contribution of periphyton to these consumers. Residuals that were not explained by sediment or nutrients were considered to be the unexplained variation. Proportions of the total variation attributed to each component were based on the adjusted (unbiased) fractions, which consider in each analysis the total number of predictors and the sample size. The significance of each fraction was tested by permutation tests using 999 randomizations (Peres-Neto et al. 2006). *p*RDA analyses were performed in the R package “vegan” using the “varpart” command (Oksanen et al. 2010).

C.2 Hierarchical partitioning

Hierarchical partitioning (HP) was used to analyze the importance of multiple predictors on maximum trophic position (MTP). This approach used R^2 values to determine the proportion of variance explained independently and jointly, by variables where all possible models in a multiple regression setting are considered (Mac Nally 2000). The predictors we tested were sediment (PC1), ecosystem size (mean stream width), mean chlorophyll-a concentrations, nitrate, and DRP (the latter three potential indicators of ecosystem productivity). Initial correlation analysis indicated that mean stream width was

more strongly correlated with MTP than cross-sectional area (CSA). The statistical significance of these variables was based on the upper 95% confidence limit (Z -score > 1.65 ; Mac Nally 2000); analyses were conducted using the “hier.part” package in R (Walsh and Mac Nally 2007).

C.3 Regression analyses

A large number of isotopic, community, and ecosystem response variables were tested with deposited sediment (PC1); these are summarized in Tables 1-3 below. Akaike Information Criterion (AIC) is a measure of the relative goodness of fit for a statistical model; the preferred model is the one with the minimum AIC value. AIC_c is AIC with a correction for finite sample sizes and the number of parameters used (Burnham & Anderson, 2002).

Residual statistics (e.g., Cook’s Distance) from regression analyses were used to identify potential outliers. Initial regression analyses of fish community Bayesian $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range with sediment indicated that one site (Waihikuawa) was a significant outlier. The data for this site were affected by low fish taxa richness, in part due to the omission of a large (820-mm body length) female long-fin eel (*Anguilla dieffenbachii*) from isotope analyses for ethical reasons. Thus, we thought it was appropriate to exclude this site from the four regressions of fish community isotopic metrics presented. This only materially affected the statistical results of one of the five regressions; the Bayesian $\delta^{13}\text{C}$ range (CR.B) with sediment. The regression with the Waihikuawa site included was not significant (LR, $F_{1,10} = 3.75$, $P = 0.082$, $R^2 = 0.273$), but the statistical power fell below 0.8 (0.423) at $\alpha = 0.05$, thus increasing the chance of a Type-II error. Removal of this site materially affected the result; (LR, $F_{1,9} = 11.7$, $P > 0.01$, $R^2 = 0.565$), but did not affect or only improved the fit of the other four regressions (mean fish species and individual SEA.B, fish NR.B and MNND.B).

Initial regression analyses indicated that one site (Courtenay) was a significant outlier for the regression of the invertebrate Bayesian $\delta^{13}\text{C}$ range (CR.B) and the mean distance to the centroid (CD.B). This site had a taxon, the hydroptilid caddisfly *Oxyethira albiceps* that possessed an extremely depleted $\delta^{13}\text{C}$ signature (-44.8 ‰). This matched the $\delta^{13}\text{C}$ value of its likely food, filamentous algae (-45.1 ‰); a carbon source that was relative uncommon at this site when we sampled on both occasions. This strongly depleted value may have been influenced by methanogenesis; groundwater aquifers can supply water supersaturated with methane to streams and rivers, providing the basis for the transfer of methane-carbon to aquatic invertebrates (Jones and Grey 2011). Consumer $\delta^{13}\text{C}$ values affected by biogenic methane may confound predictions regarding consumer-resource interactions (as measured by $\delta^{13}\text{C}$ range) and sedimentation. There is also evidence that stream benthos in stagnant backwater pools can derive up to 30% biomass carbon from methane (Kohzu et al. 2004).

Nevertheless, this site (Courtenay) was omitted from the CR.B regression because its exclusion did not materially affect the statistical results, although it did improve the fit of the relationship. The Bayesian centroid distance (CD.B) for the invertebrate community showed a weakly negative non-significant relationship with sediment (LR, $F_{1,10} = 3.89$, $P = 0.077$, $R^2 = 0.280$). This result was strongly influenced by one outlying site (Courtenay), and the statistical power fell below 0.8 (0.423) at $\alpha = 0.05$, thus increasing the chance of a Type-II error. Excluding this site changed the result; invertebrate CD.B was negatively associated with sediment (LR, $F_{1,9} = 16.7$, $P < 0.01$, $R^2 = 0.649$).

LITERATURE CITED

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

- Jones, R. I., and J. Grey. 2011. Biogenic methane in freshwater food webs. *Freshwater Biology* 56:213-229.
- Kohzu, A., C. Kato, T. Iwata, D. Kishi, M. Murakami, S. Nakano, and E. Wada. 2004. Stream food web fueled by methane-derived carbon. *Aquatic Microbial Ecology* 36:189-194.
- Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation* 9:655-671.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner 2010. *Vegan: community ecology package*. R Foundation for Statistical Computing, Vienna, Austria.
- Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614-2625.
- Walsh, C., and R. Mac Nally 2007. *Hierarchical Partitioning*. R Foundation for Statistical Computing, Vienna, Austria.

TABLE C1. Summary of regression analyses testing the effects of sediment (PC1) on selected isotopic responses. Arrows indicate the direction of significant relationship (e.g., ↓↑ indicates a ‘U’-shaped relationship), numbers indicate ΔAIC_c (i.e., $AIC_c^i - AIC_c^j$, where i is the AIC_c value for the given model, and j is the minimum AIC_c recorded).

SIA community metrics		Total		Invert		Fish	
		Linear	Linear	3-parameter exponential	3-parameter logistic	Linear	Quadratic
$\delta^{15}\text{N}$ range	NR.B	ns	ns			↓	
$\delta^{13}\text{C}$ range	CR.B	↓	↓	3.91	3.71	↓	
Trophic area	THA.B	↓	↓			n/a	
Centroid distance	CD.B	↓	↓			n/a	
Nearest neighbor distance	NND.B	ns	ns			6.70	↓↑
NND standard deviation	SDNND.B	ns	ns			n/a	
Standard ellipse area	SEA.B <i>spp</i>	↓	↓			13.9	↓↑
	SEA.B <i>indv</i>	n/a	n/a			13.5	↓↑

TABLE C2. Regression analyses testing effects of sediment (PC1) on community responses. Arrows, direction of significant relationships (e.g., $\uparrow\downarrow$ indicates a ‘hump-backed’-shaped relationship); numbers, ΔAIC_c (i.e., $AIC_c^i - AIC_c^j$, where i is the model AIC_c , and j is the minimum AIC_c recorded). EPT, sediment-sensitive insect orders (Ephemeroptera, Plecoptera, Trichoptera); FFGF, functional feeding group trait frequency; FFGA; functional feeding group trait affinity (trait frequency per taxon/individual); SIA, stable isotopes analysis; TF, trait frequency; TA, trait affinity.

Community	Response	Linear	Logistic	Power	Exponential	Quadratic	Asymptotic exponential	3-parameter logistic	4-parameter sigmoidal
Total	Richness	4.52				2.55		↓	
Fish	Richness	1.35				$\uparrow\downarrow$		0.53	
Invert.	Taxa richness	2.46				2.22		↓	
	EPT richness	↓							
	Rarefied EPT richness	ns							
	% EPT	5.24	3.66				2.68	↓	5.13
	log ‘Grazer’ FFGF	↓							
	log ‘Shredder’ FFGF	↓							
	Abundance ‘collector’ FFGA	5.30	↑			2.21			
	Occupancy ‘collector’ FFGA	↑							
	SIA ‘collector’ FFGA	↑							
	‘Omnivore’ TF	↓							
	‘Deposit-feeder’ TF	↑							
	‘Deposit-feeder’ TA	1.04		↑	1.52			2.57	8.25

TABLE C3. Regression analyses testing effects of sediment (PC1) on community responses. Arrows indicate direction of significant relationships, numbers indicate ΔAIC_c (i.e., $AIC_{ci} - AIC_{cj}$, where i is the model AIC_c , and j is the minimum AIC_c recorded). log, $\log(x + 1)$; FBOM, fine benthic organic matter (g/m²); Chl-a, chlorophyll-a concentrations ($\mu\text{g}/\text{cm}^2$); CPOM, coarse particulate matter; C/N, molar carbon:nitrogen; SIA, stable isotopes analysis; PC, primary consumer; % periphyton, relative proportion of reliance on periphyton resources.

Ecosystem response		Linear	Logistic
Basal resource	log FBOM	↑	
	log Chl-a : FBOM	↓	
	log CPOM : FBOM	↓	
Resource stoichiometry	Periphyton C/N	2.4	↑
	FBOM C/N	↑	
	CPOM C/N	ns	
	SFPM C/N	ns	
SIA mixing models	PC % periphyton	↓	
	'Shredder' % periphyton	ns	
	'Grazer' % periphyton	↓	
	'Collector' % periphyton	↓	

APPENDIX D. Additional results from analyses of community data.

TABLE D1. Results from principal components analyses (PCA) used to a) summarize influences of physico-chemical variables (excluding sediment and nutrients) on study sites and b) reduce measured sediment variables to a single index (PC1). SIS, suspendable inorganic sediment.

PCA Model		PCA Axis 1	PCA Axis 2
Physico-chemical	% Variation	40.2	20.0
	<i>Eigenvectors</i>		
	Flow (m/s)	-0.34	-0.58
	Wetted width (m)	0.20	-0.91
	Depth (m)	-0.85	0.09
	Maximum depth (m)	-0.90	0.23
	Dissolved oxygen (mg/L)	0.99	0.20
	pH	0.54	-0.53
	Temperature (°C)	0.75	0.47
Sediment	% Variation	85.0	12.7
	<i>Eigenvectors</i>		
	Reach sediment (% cover)	-0.53	-0.26
	Patch sediment (% cover)	-0.49	-0.61
	log SIS (g/m ²)	-0.46	0.73
	log Depth (mm)	-0.52	-0.52

TABLE D2. Pearson product-moment correlations (r) of non-metric dimensional scaling (NMDS) Axis 1 scores from invertebrate community data. Abundance, individuals/0.0625 m²; occupancy, presence-absence; SIA, invertebrates selected for stable isotope analysis (occupancy data). ** $P < 0.01$, *** $P < 0.001$

NMDS Axis 1	Sediment (PC1)	Abundance	Occupancy	SIA
Sediment (PC1)	1			
Abundance	0.96***	1		
Occupancy	0.79**	0.90***	1	
SIA	0.82**	0.92***	0.87***	1

TABLE D3. Summary of results from regression analyses of ‘fuzzy’-coded invertebrate functional feeding groups (FFG) and feeding traits. Frequency refers to aggregated trait scores; affinity is the frequency per individual or taxon. Abundance, individuals/0.0625 m²; occupancy, presence-absence; SIA, invertebrates selected for stable isotopes analysis (occupancy data).

Functional feeding traits		Trait response	Invertebrate community data		
			Abundance	Occupancy	SIA
FFGs	‘Shredder’	Frequency	↓	ns	↓
		Affinity	ns	ns	↓
	‘Grazer’	Frequency	↓	↓	↓
		Affinity	↓	↓	ns
	‘Collector’	Frequency	ns	ns	ns
		Affinity	↑	↑	↑
	‘Predator’	Frequency	ns	ns	ns
		Affinity	ns	ns	ns
Feeding generalists	‘Omnivore’	Frequency	↓	↓	ns
		Affinity	ns	ns	ns
	‘Polyphage’	Frequency	ns	ns	ns
		Affinity	ns	ns	ns
Habitat	‘Deposit-feeder’	Frequency	↑	ns	↑
		Affinity	↑	↑	↑
	‘Rheophile’	Frequency	↓	↓	↓
		Affinity	↓	↓	↓

APPENDICES

CHAPTER 4

APPENDIX A. Detritivorous caddisfly taxa.

TABLE 1. Detritivorous caddisfly taxa collected from 9 streams on the Canterbury Plains during the austral summer of 2010/2011 that contribute to ‘shredding’ of leaf litter. FFG, functional-feeding group.

Family	Taxa	‘Shredder’	Other FFG
Conoesucidae	<i>Olinga feredayi</i>	Facultative	Collector
	<i>Pycnocentria evecta</i>	Facultative	Collector
Leptoceridae	<i>Hudsonema alienum</i>	Facultative	Predator
	<i>Hudsonema amabile</i>	Facultative	Predator
	<i>Triplectides obsoletus</i>	Obligate	
Oeconesidae	<i>Oeconesus</i> sp.	Obligate	

APPENDIX B. Results from leaf-pack analyses.

TABLE B1. Results of linear mixed-effects models (LMEM) testing the associations of leaf pack treatments (open, case protected, and buried) and sediment variables (% sediment cover and the sediment ratio with response variables recorded from leaf packs collected on Day 72 (April 2011) from nine streams on the Canterbury Plains, New Zealand during the austral summer of 2010-2011. The sediment ratio refers to the amount of inorganic material <2 mm relative to remaining leaf litter at Day 72. 1.0E-01 is an abbreviated form of 1.0×10^{-1} .

Response	Predictors	Value	SE	df	<i>t</i>	<i>p</i>
Sediment ratio (g inorganics g ⁻¹ AFDM litter)	(Intercept)	0.30	0.16	63	1.89	0.06
	Protected	0.28	0.13	63	2.14	< 0.05
	Buried	-0.24	0.12	63	-1.94	0.06
	Sediment cover (%)	0.36	0.37	7	0.97	0.36
	Protected × cover	-0.64	0.31	63	-2.02	< 0.05
	Buried × cover	1.58	0.30	63	5.20	< 0.001
Litter breakdown (<i>k_{dd}</i> , g AFDM degree day ⁻¹)	(Intercept)	1.7E-03	2.0E-04	67	8.67	< 0.001
	Protected	-7.6E-04	1.7E-04	67	-4.53	< 0.001
	Buried	-6.4E-04	1.9E-04	67	-3.39	< 0.01
	Sediment cover (%)	-1.8E-03	4.4E-04	7	-4.11	< 0.01
	Protected × cover	9.3E-04	3.7E-04	67	2.53	< 0.05
	Buried × cover	2.2E-04	4.1E-04	67	0.54	0.59
	(Intercept)	-7.05	0.16	62	-43.29	< 0.001
	Protected	-0.50	0.17	62	-2.90	< 0.01
	Buried	-0.27	0.18	62	-1.49	0.14
	Sediment ratio	0.18	0.18	62	1.02	0.31
	Protected × sediment	-0.006	0.27	62	-0.20	0.98
	Buried × sediment	-0.87	0.27	62	-3.17	< 0.01
Microbial activity (O ₂ mg L ⁻¹ hr ⁻¹ g ⁻¹ AFDM leaf)	(Intercept)	1.18	0.10	68	11.41	< 0.001
	Protected	-0.03	0.02	68	-1.22	0.23
	Buried	-0.22	0.02	68	-9.37	< 0.001
	Sediment cover (%)	-0.15	0.23	7	-0.68	0.52
	(Intercept)	1.14	0.04	63	27.23	< 0.001
	Protected	-0.02	0.03	63	-0.89	0.38
	Buried	-0.21	0.03	63	-8.31	< 0.001
	Sediment ratio	-0.04	0.03	63	-1.58	0.12

TABLE B2. Results of LMEM describing the associations of leaf pack treatments (open, protected, and buried) and sediment variables (% cover and sediment ratio) with leaf pack invertebrate community composition. Community composition using Axis 1 scores from non-metric dimensional scaling (NMDS) analyses were calculated from leaf pack invertebrate densities. For the model including % sediment cover, community composition data was used from leaf packs collected at Days 7, 21 and 72 (January – April 2011) from nine streams on the Canterbury Plains, New Zealand during the austral summer of 2010-2011; the sediment ratio model used community composition data recorded from leaf packs collected on Day 72.

Response	Predictors	Value	SE	df	<i>t</i>	<i>p</i>
Community composition (NMDS Axis 1 scores)	(Intercept)	2.74	0.39	70	7.07	< 0.001
	Protected	-0.19	0.10	70	-1.98	0.052
	Buried	-0.38	0.10	70	-3.90	< 0.001
	Sediment cover (%)	-2.02	0.85	7	-2.38	< 0.05
	(Intercept)	1.83	0.22	62	8.25	< 0.001
	Protected	-0.33	0.18	62	-1.80	0.08
	Buried	1.24	0.23	62	5.42	< 0.001
	Sediment ratio	0.12	0.22	62	0.54	0.59
	Protected × sediment	-0.20	0.35	62	-0.57	0.57
	Buried × sediment	-0.72	0.28	62	-2.52	< 0.05

TABLE B3. Results of LMEM describing the associations of leaf pack treatments (open, protected, and buried) and sediment variables (% cover and sediment ratio) with detritivorous caddisflies. For the model including % sediment cover, detritivorous caddisfly richness (rarefied) and density data were used from leaf packs collected at Days 7, 21 and 72 (January – April 2011) from nine streams on the Canterbury Plains, New Zealand during the austral summer of 2010-2011; the sediment ratio model used invertebrate data recorded from leaf packs collected on Day 72.

Response	Predictors	Value	SE	df	<i>t</i>	<i>p</i>
Detritivorous caddisfly richness (rarefied taxa g ⁻¹ AFDM litter)	(Intercept)	3.39	0.31	175	10.92	< 0.001
	Protected	-1.11	0.26	175	-4.20	< 0.001
	Buried	1.03	0.27	175	-3.92	< 0.001
	Sediment cover (%)	-4.39	0.64	7	-6.81	< 0.001
	Protected × cover	1.45	0.51	175	2.82	< 0.01
	Buried × cover	1.39	0.51	175	2.69	< 0.01
	(Intercept)	0.78	0.32	62	2.44	< 0.05
	Protected	0.23	0.21	62	1.13	0.26
	Buried	1.42	0.27	62	5.27	< 0.001
	Sediment ratio	0.45	0.27	62	1.67	0.10
	Protected × sediment	-0.18	0.40	62	-0.44	0.66
	Buried × sediment	-1.05	0.35	62	-3.02	< 0.01
Detritivorous caddisfly density (individuals g ⁻¹ AFDM litter)	(Intercept)	0.88	0.09	175	9.45	< 0.001
	Protected	-0.64	0.10	175	-6.44	< 0.001
	Buried	0.38	0.19	175	1.95	0.05
	Sediment cover (%)	-1.15	0.21	7	-5.59	< 0.001
	Protected × cover	0.83	0.22	175	3.75	< 0.001
	Buried × cover	-0.71	0.43	175	-1.64	0.10
	(Intercept)	0.78	0.32	62	2.44	< 0.05
	Protected	0.23	0.21	62	1.13	0.26
	Buried	1.42	0.27	62	5.27	< 0.001
	Sediment ratio	0.45	0.27	62	1.67	0.10
	Protected × sediment	-0.18	0.40	62	-0.44	0.66
	Buried × sediment	-1.05	0.35	62	-3.02	< 0.05

TABLE B4. Results of LMEM describing the associations of leaf pack treatments (open, protected, and buried) and biotic influences (detritivorous caddisfly densities and microbial activity) on litter breakdown (k_{dd} , g AFDM degree day⁻¹). Leaf microbial activity (O₂ mg L⁻¹ hr⁻¹ g⁻¹ AFDM leaf) and detritivorous caddisfly densities (individuals g⁻¹ AFDM litter) were recorded from leaf packs collected on Day 72 (April 2011) from nine streams on the Canterbury Plains, New Zealand during the austral summer of 2010-2011. 1.0E-01 is an abbreviated form of 1.0×10^{-1} .

Response	Predictors	Value	SE	df	<i>t</i>	<i>p</i>
Litter breakdown (k_{dd} , g AFDM degree day ⁻¹)	(Intercept)	6.6E-04	6.4E-05	68	10.20	< 0.001
	Protected	-1.1E-04	2.7E-05	68	-4.02	< 0.001
	Buried	-4.0E-04	3.1E-05	68	-12.80	< 0.001
	Detritivore density	5.5E-05	1.6E-05	68	-3.37	< 0.01
	(Intercept)	1.2E-03	2.1E-04	68	5.75	< 0.001
	Protected	-3.6E-04	7.2E-05	68	-5.03	< 0.001
	Buried	-5.8E-04	9.3E-05	68	-6.27	< 0.001
	Microbial activity	2.2E-05	1.6E-04	68	-1.39	0.17

APPENDIX C. Results from Experiment 1 randomized block ANOVAs.

TABLE 1. Results of randomized block ANOVAs testing the factorial effects of experimental treatments (presence/absence of sediment and the detritivorous caddisfly *Triplectides obsoletus*) on litter breakdown rates, production of fine organic particulate matter (FPOM; 45-250 μm), leaf microbial respiration, and invertebrate responses. Post-hoc differences were tested using Tukey's HSD. Body mass_m, metabolic body mass (or body mass^{0.75}); 1.0E-01 = 1.0×10^{-1} .

Response	Predictor	df	SS	MS	F-value	Pr(>F)
Litter mass loss (mg AFDM day ⁻¹)	Treatment	3	1387	462.4	47.2	< 0.001
	Block	3	25	8.3	0.8	0.48
	Residuals	41	382	9.8		
FPOM production (mg AFDM day ⁻¹)	Treatment	3	534	178.0	239.7	< 0.001
	Block	3	0.9	0.3	0.4	0.74
	Residuals	41	30.4	0.7		
Microbial activity (O ₂ mg L ⁻¹ hr ⁻¹ g ⁻¹ AFMD leaf)	Treatment	3	21.5	7.2	1.0	0.40
	Block	3	32.3	10.8	1.5	0.23
	Residuals	41	284	7.1		
Litter mass loss per body mass (mg day ⁻¹ mg ⁻¹ body mass _m)	Treatment	1	2.1E-03	2.1E-03	0.1	0.74
	Block	3	9.3E-02	3.1E-02	1.7	0.20
	Residuals	19	3.5E-01	1.9E-02		
FPOM production per body mass (mg day ⁻¹ mg ⁻¹ body mass _m)	Treatment	1	1.6E-04	1.6E-04	0.0	0.86
	Block	3	1.8E-02	6.1E-03	1.1	0.37
	Residuals	19	1.0E-01	5.4E-03		
Total biomass (g AFDM)	Treatment	1	6.5E-05	6.5E-05	1.8	0.19
	Block	3	1.8E-04	6.0E-05	1.7	0.21
	Residuals	19	6.8E-04	3.6E-05		
Mean individual biomass (g AFDM)	Treatment	1	3.0E-07	3.0E-07	0.2	0.70
	Block	3	1.1E-05	3.8E-06	1.9	0.16
	Residuals	19	3.7E-05	2.0E-06		
Growth (mg exuviae day ⁻¹ mg ⁻¹ mass _m)	Treatment	1	1.6E-07	1.6E-07	4.5	< 0.05
	Block	3	4.3E-08	1.4E-08	0.4	0.75
	Residuals	19	6.5E-07	3.4E-08		
% Mortality	Treatment	1	1276	1276	6.7	< 0.05
	Block	3	1328	443	2.3	0.11
	Residuals	19	3620	191		

APPENDIX D. Results from Experiment 2 analyses (LMEM and GLMM).

TABLE D1. Results of linear mixed-effects models (LMEM) testing the influence of deposited sediment and detritivore identity (mid-late instar larvae of a conoesucid caddisfly *Olinga feredayi*, and a leptocerid caddisfly *Triplectides obsoletus*) on detrital resources and leaf microbial activity recorded from microcosm laboratory Experiment 2. Body mass_m, metabolic body mass (or body mass^{0.75}); *p*MCMC, Markov chain Monte Carlo (MCMC)-estimated *p*-values considered significant at $\alpha < 0.05$.

Response	Predictor	Value	SE	df	<i>t</i>	<i>p</i> MCMC
Litter mass loss (mg AFDM day ⁻¹)	(Intercept)	33.43	2.22	41	15.05	< 0.001
	<i>Triplectides</i>	12.59	1.24	41	10.15	< 0.001
	Sediment	-10.80	1.97	41	-5.48	< 0.001
FPOM production (mg AFDM day ⁻¹)	(Intercept)	6.02	0.65	40	9.32	< 0.001
	<i>Triplectides</i>	10.8	0.88	40	12.3	< 0.001
	Sediment	-2.34	1.08	40	-2.16	< 0.05
	<i>Triplectides</i> × sediment	-4.97	1.58	40	-3.14	< 0.01
Microbial activity (O ₂ mg L ⁻¹ hr ⁻¹ g ⁻¹ AFMD leaf)	(Intercept)	4.92	0.46	41	10.6	< 0.001
	<i>Triplectides</i>	0.76	0.46	41	1.66	0.11
	Sediment	-1.24	0.71	41	-1.75	0.09
Litter mass loss per body mass (mg day ⁻¹ mg ⁻¹ body mass _m)	(Intercept)	0.60	0.09	40	6.65	< 0.001
	<i>Triplectides</i>	-0.11	0.10	40	-1.12	0.28
	Sediment	0.24	0.12	40	2.04	0.051
	<i>Triplectides</i> × sediment	-0.45	0.18	40	-2.56	< 0.05
FPOM production per body mass (mg day ⁻¹ mg ⁻¹ body mass _m)	(Intercept)	0.10	0.014	40	7.24	< 0.001
	<i>Triplectides</i>	0.093	0.020	40	4.73	< 0.001
	Sediment	0.017	0.024	40	0.71	0.47
	<i>Triplectides</i> × sediment	-0.12	0.035	40	-3.48	< 0.001

TABLE D2. Results of LMEM testing the effects of deposited sediment and detritivore identity (mid-late instar larvae of a conoesucid caddisfly, *Olinga feredayi* and a leptocerid caddisfly *Triplectides obsoletus*) on selected invertebrate responses recorded from microcosm laboratory Experiment 2. Body mass_m, metabolic body mass (or body mass^{0.75}); *p*MCMC, Markov chain Monte Carlo (MCMC)-estimated *p*-values considered significant at $\alpha < 0.05$.

Response	Predictor	Value	SE	df	<i>t</i>	<i>p</i> MCMC
Total biomass (g AFDM)	(Intercept)	0.022	0.0032	40	7.19	< 0.001
	<i>Triplectides</i>	0.020	0.0045	40	4.30	< 0.001
	Sediment	-0.009	0.0055	40	-1.61	0.10
	<i>Triplectides</i> × sediment	0.018	0.0080	40	2.24	< 0.05
Mean individual biomass (g AFDM)	(Intercept)	0.0025	3.2E-04	40	6.90	< 0.001
	<i>Triplectides</i>	0.0019	5.1E-04	40	3.67	< 0.001
	Sediment	-0.0010	6.4E-04	40	-1.63	0.11
	<i>Triplectides</i> × sediment	0.0033	9.3E-04	40	3.53	< 0.001
Minimum individual biomass (g AFDM)	(Intercept)	4.7E-04	2.1E-04	40	2.23	< 0.05
	<i>Triplectides</i>	9.0E-04	3.0E-04	40	2.98	< 0.01
	Sediment	-1.7E-04	3.7E-04	40	-0.45	0.66
	<i>Triplectides</i> × sediment	1.5E-04	5.3E-04	40	2.89	< 0.01
Maximum individual biomass (g AFDM)	(Intercept)	0.0042	0.0015	40	2.80	< 0.01
	<i>Triplectides</i>	0.0120	0.0015	40	8.03	< 0.001
	Sediment	0.0013	0.0023	40	0.57	0.57
Growth (mg exuviae day ⁻¹ mg ⁻¹ body mass _m)	(Intercept)	0.388	0.033	40	11.6	< 0.001
	<i>Triplectides</i>	-0.125	0.0580	40	-3.80	< 0.001
	Sediment	-0.193	0.0716	40	-3.72	< 0.001
<i>Olinga</i> case growth (% increase)	(Intercept)	25.0	2.85	18	8.76	< 0.001
	Sediment	-16.2	3.32	18	-4.86	< 0.001

TABLE D3. Results of binomially-distributed generalized linear mixed-effects models (GLMM) testing the effects of deposited sediment on % mortality rates of detritivores recorded from microcosm laboratory Experiment 2. Two different detritivores were used; mid-late instar larvae of a conoesucid caddisfly *Olinga feredayi* and a leptocerid caddisfly *Triplectides obsoletus*.

Response	Predictor	Estimate	SE	z value	Pr(> z)
Mortality (Model 1)	(Intercept)	-4.61	0.99	-4.66	< 0.001
	<i>Triplectides</i>	1.64	1.03	1.59	0.11
	Sediment	1.12	1.41	0.79	0.43
	<i>Triplectides</i> × sediment	0.54	1.56	0.35	0.73
Mortality (Model 2)	(Intercept)	-3.40	0.50	-6.83	< 0.001
	<i>Olinga</i> × sediment	-0.60	0.96	-0.62	0.53
	<i>Triplectides</i> × sediment	2.25	0.61	3.70	< 0.001